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STUDIES ON NEMATODE GAMETOGENESIS

By

Arthur Calvin Walton

A. B. Northwestern University, 1913
A. M. Northwestern University, 1915

THESIS

SUBMITTED IN PARTIAL FULFILLMENT OF THE REQUIREMENTS FOR THE DEGREE OF DOCTOR OF PHILOSOPHY IN ZOOLOGY IN THE GRADUATE SCHOOL OF THE UNIVERSITY OF ILLINOIS, 1923

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Erratum.

In	line	11	page	169	read	"*Contracaecum*"	instead	of	"*Contraceecum*",
„	„	20	„	171	„	"Sycon sponges"	„	„	"Romen type",
„	„	42	„	172	„	"*Culex*"	„	„	"ITALIS",
„	„	31	„	179	„	"*Contracaecum*"	„	„	"*Caontracecum*",
„	„	21	„	180	„	"*lumbricoides*"	„	„	"*lmbricoides*",
„	„	42	„	213	„	"Agar"	„	„	"Rom",
„	„	25	„	217	„	"*univalens*"	„	„	"itolis",
„	„	23	„	235	„	"diameters"	„	„	"diametra".

STUDIES ON NEMATODE GAMETOGENESIS[1].

By

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University of Illinois.

With Plates VIII—XI and 2 Textfigures.

(Eingegangen am 12. Januar 1923.)

I. Introduction.

The work in this paper on the Comparative Gametogenesis of certain parasitic nematodes is an attempt to throw further light on the question of multiple or compound chromosomes earlier noted in *Ascaris canis* (WALTON, 1916a, 1918). An attempt is also made to determine what correlation, if any, exists between cytological phenomena and the taxonomy of the nematodes studied.

The writer here wishes to express his appreciation to Prof. Dr. H. B. WARD, Director of the Zoological Laboratories of the University of Illinois, not only for the priveleges afforded by the use of the Laboratories, but also for his personal interest and assistance. Thanks are also due to other members of the staff and to fellow students for assistance in collecting material and also for the loan of valuable specimens for comparative study. Many of the identifications were made by the Bureau of Animal Husbandry, U. S. Department of Agriculture, and the writer wishes to here express his appreciation for the service rendered.

II. Literature.

The parasitic nematodes, especially the Ascarids, have been recognized as excellent material for cytological study since 1850, culminating in the classical work of BOVERI, VAN BENEDEN and others in the last decade of the nineteenth century. The importance of the nematodes from the medical standpoint has turned attention to their physiological rather than to their cytological structures during recent years.

In 1891, HENKING, working on the insect Pyrrhocoris, first noted an extra chromatic body in one-half of the spermatozoa which the later studies of PAULMIER (1899), MONTGOMERY (1901) and DE SINÉTY (1901) on other insects showed to be a true chromosome. MCCLUNG (1902) suggested

[1]) Contributions from the Zoological Laboratory of the University of Illinois, under the Direction of HENRY B. WARD, No. 239.

that this chromosome might in some way be connected with the determination of sex and later researches, both cytological and genetical, have substantiated this supposition.

The Nematodes, because of their well-known favorableness as cytological material, were the next group after the Insects to be critically studied to determine the presence or absence of these so-called sex-chromosomes. Boveri (see Gulick, 1911) found a single, unpaired X chromosome in a species of Heterakis taken from a pheasant. Boring (1909) discovered a consistantly appearing extra chromosome in the males of on especimen of *Ascaris megalocephala* which Boveri interpreted as an unpaired X chromosome that normally is attached to an autosome and hence usually invisible. Edwards (1910b) clearly substantiated the contention of Boveri as to the presence of an identifiable X element in the chromosomes of the male of *A. megalocephala*. Edwards also found an X group consisting of five members to be present during spermatogenesis of *A. lumbricoides*. Frolowa (1912) reported the presence of identifiable 2X conditions in ninety per-cent of the eggs of *A. megalocephala*. Geinitz (1915) also came to the same conclusion. Gulick (1911) found a single X element in the male germ cells of the following Nematodes: *Heterakis dispar*, *H. inflexa*, *H. vesicularis*, *Strongylus paradoxus* and *S. tenuis*. The reduction division for the heterochromosome was the first in each case, except *S. tenuis* in which the second division apparently was reductional. Boveri (1911) and Schleip (1911) found two kinds of spermatozoa, differing by one X element, in the sex cells formed by the males of both the free living and the parthenogenetic generations of *Angiostomum nigrovenosum*. Edwards (1911) described a case of an X-Y condition in *Ascaris felis*. Boveri interpreted this as an X condition in which the X was attached to an autosome. Walton (1921) has shown that the latter interpretation is the more logical. Mulsow (1912), working on the gemetogenesis of *Ancyracanthus cystidicola*, reported the presence of a single X chromosome in the male. Krüger (1913) described a peculiar case found in *Rhabditis aberrans*, in which all of the females develop parthenogenetically, retaining the diploid number of chromosomes — eighteen — by undergoing only one polar division. This worm is proterandrously hermaphroditic and produces both eggs and sperm in each individual. Two types of spermatozoa are formed, neither of which function. The spermatogonia all contain eighteen chromosomes which reduce to eight paired and two unpaired bodies in Spermatocyte I. The first division is equational for the unpaired bodies and reductional for the others, thus furnishing ten chromosomes to each second spermatocyte. The second division is reductional for the heterochromosomes, each spermatid receiving nine (8 +acc.). In half of the spermatozoa, the accessory

chromosome is lost in the "residual body" as is the case in *Angiostomum nigrovenosum* (SCHLEIP, 1912). Although KRÜGER offered no explanation of the phenomenon, it resembles very closely an X-Y condition in which the Y is eventually lost. In this case the X is likewise functionless although retained in the spermatozoon nucleus.

KÜHTZ (1913), in a study of *Sclerostomum edentatum* and *S. equinum*, found a single X chromosome present. The two types of spermatozoa possessed five and six chromosomes respectively, while the egg showed six. MEVES (1915), in *Filaria papillosa*, and (1921), in *Oxyuris ambigua*, found a single X chromosome present in one-half of the spermatozoa. GOODRICH (1914, 1916), working on *Ascaris incurva* (now *Contraceecum incurvum*), described the most complex heterochromosome group that has as yet been reported for the Nematodes. He found an X-Y group in which the single Y element is paired with eight X elements — giving two types of spermatozoa having the following formulae: 13 + 8 X and 13 + Y. Each egg has the the formula 13 + 8 X, giving rise, after fertilization by the two sorts of spermatozoa, to two kinds of embryos: —26 + 8 X + Y = 35 (male) and 26 + 16 X = 42 (female). The Y is attached to one of the members of the X group, separating at the second division. WALTON (1916a) observed an X group containing six members in the spermatogenesis of *Ascaris canis* (now *Toxascaris canis*), and later (1918) described the 2 X condition of twelve members which obtained during oogenesis. The same investigator (1921) confirmed the earlier predictions of BOVERI (see EDWARDS, 1911) by describing the 2 X condition found in the eggs of *Ascaris felis* (now *Belascaris mystax*). KRÖNING (1923), working on *Rhabditis aspera*, *R. pellio* BÜTSCHLI, *R. pellio* SCHNEIDER, *Strongylus filaria*, *S. paradoxus* and *S. micrurus* found a single X chromosome in each case.

Several earlier writers noted sexual differences in chromosome numbers and behavior, but as the sex-chromosome was not clearly understood or even recognized in some cases, no mention of them was made. MARCUS (1906) found some of the spermatozoa of *Ascaris mystax* to contain one less chromosome than the rest and that two chromosomes failed to pair during early spermatogenesis as did the other twenty. STRUCKMAN (1905) figured (Taf. 30, Abb. 45-47) a tetrad chromosome which lagged behind during the first maturation division but eventually divided. This simulates the action of an X-Y pair separating at the first division, or that of an autosome delayed in division because of an attachment to an X body. Such a lagging condition was observed at the time of the first division in the spermatogenesis of both *Strongylus filaria* and *S. paradoxus*.

Much study has been devoted to the history of the sex-chromosome and some evidence of the physical separation of autosomes and karyo-

somes during portions or all of the germ cycle has been accumulated. The physiological entity has long been recognized for the heterochromosomes, but less is known of the actual physical separation between the two kinds of chromatic material. In most cases, e. g., Anasa, Harmostes, Alydus, Euschistus, Coenus and Podisus among Hemiptera (Wilson, 1906), and Ancyracanthus, a nematode (Mulsow, 1912), the sex-chromosomes are recognizably isolated in the male but not in the female. Besides Ancyracanthus, other nematodes to show the presence of a separate karyosome for the heterochromosomes are *Ascaris canis* (Walton, 1916a, 1918); *A. felis* (Walton, 1921); *A. incurva* (Goodrich, 1914, 1916); *A. megalocephala* (Boveri, 1909b; Geinitz, 1915); *Heterakis dispar*, *H. inflexa*, *H. vesicularis* and *Strongylus paradoxus* (Gulick, 1911).

Boveri (1892) described the peculiar diminution process which appeared in the cleavage stages of *Ascaris megalocephala*. Meyer (1895) reported the same conditions in *A. lumbricoides*, *A. rubicunda* and *A. labiata*. Goodrich (1916) found diminution in *A. incurva* and Walton (1918) in *A. canis*. Several workers have reported the loss of portions of chromatic material, both before and after fertilization, other than by diminution. Chief of these methods is the so-called „cytophore" formation during the metamorphosis of the spermatid, wich has been reported for *Ancyracanthus cystidicola* (Mulsow, 1912), *Angiostomum nigrovenosum* (Boveri, 1911; Schleip, 1911), *Ascaris megalocephala* (Hertwig, 1890; Mayer, 1908) and *A. mystax* (Marcus, 1906).

The question of variation of numbers of the chromosomes in different tissues of the body has been attacked by numerous workers and interpreted in several ways. The two main theories have been those of fragmentation and of compound chromosomes, the chief differences being in the idea as to the nature of the multiplication of the numbers. Agar (Textbook of Cytology, 1920) maintains that the chromosomes of the "germ-track" always contain the basic number for any species, but that those of the soma fragment in many, if not all, of the cells. He bases his argument upon the fact that the soma cells do not contain any definite number of chromosomes, but that the various parts are equal in volume to those of the compact germ cell chromosomes. Hance (1917) in the pig and in Oenothera gives convincing proof that such a condition actually prevails. Various insects also show this same phenomenon. Agar includes the "diminution" process of *Ascaris megalocephala*, *A. canis*, and *A. nigrovenosa* in the same class with "fragmentation". Walton (1918) argues that the presence of a definite increased number of chromosomes in the soma cells such as always accompanies diminution points to another interpretation applicable to a large number of cases: that of compound or fused chromosomes in the germ cells which may be reduced to their simple condition in

the somatic cells of the embryo. This explanation does not obviate that of fragmentation, but holds that the soma cells originally showed the simple number and that the germ cells were specialized from that number. The soma cells may occasionally show fragmentation but the germ cell chromosome number is not necessarily the primitive number for the species. The germ cells may keep the primitive number, and probably do so in the majority of cases, but not necessarily. In support of this view, WALTON states that the presence of a Querkerbe (earlier studied by HÄCKER, 1895, 1911; KORNHAUSER, 1914, 1915; JÖRGENSEN, 1910 *et alii*) may be the visible indication of the point of union of the various somatic chromosomes into the compacted type of the germinal cells. This he believes to have been definitely shown in his study of *Ascaris canis*. The formation of di-tetrad or octad chromosomes, either morphologically or physiologically, is further evidence of this fused condition of the chromosomes, showing not only the union of the pairs of homologous chromosomes during pseudoreduction, but also that each one of the two chromosomes was a complex structure before it became attached to its mate in Prophase I. Such di-tetrads have been reported in Cyclops (HÄCKER, 1895; BRAUN, 1909), in Copepods (KRIMMEL, 1910; MATSCHECK, 1910) and in Romen type (JÖRGENSEN, 1910) as well as in *Ascaris mystax* (MARCUS, 1906) and *A. canis* (WALTON, 1916a, 1918). The simplest germ cell chromosomes in such cases are double structures. In the case of the Ascarids, these reduce to a simple monad condition of twice the diploid number of monad chromosomes. The soma cell chromosomes are definite in number in these cases and represent the primitive condition as to chromosome number rather than represent any fragmentation process. Other nematodes show a definite increased number of somatic chromosomes over the germ-cell number, the ratio in some cases rising to twenty-six to one. BLANKERTZ, (1910) has shown that each of the germ cell chromosomes of *Ascaris megalocephala* is at least a twelve-parted compound body. SCHLEIP (1912) has shown that the simplest germ cell chromosome of *Angiostomum nigrovenosum* is double in structure. One of the Gall Flies — *Neuroterus lenticularis* —, a solitary wasp — *Osmia cornuta* —, and the bee — *Apis mellifica* show similar phenomena. BONNEVIE (1902) shows that the rod-shaped zygote chromosomes of *Ascaris lumbricoides* are three-parted, two of which are lost at the time of the diminution division, and the other — the middle one of the three — is retained. Both soma and germ cells thus show the same number of chromosomes, but those of the soma cells are only one-third the volume of those in the germ cells. MARCUS (1906) gives a series showing the degree of fusion of the somatic chromosomes as found in the germ cells of several nematodes. The somatic numbers are as follows: *Ascaris megalocephala*, 60 and 70; *A. lumbricoides*, 48;

A. clavata, 48; *A. mystax*, 44; The germ cell numbers are: *A. lumbricoides*, 24; *A. clavata*, 24; *A. mystax*, 22; *A. megalocephala bivalens*, 4; and *A. megalocephala univalens*, 2. He suggests that these might represent a phylogenetical series in the gradual fusion of the germ-cell chromosomes.

A peculiar group of cases of the reduction of the chromosome number needs special consideration. These fall under two heads: (1). There are apparently two pseudoreductions, caused by the pairing of homologous chromosomes during the prophase of each of the two meiotic divisions, giving one-fourth of the diploid number as the number found in Metaphase II. In practically all cases these pairs separate to form the haploid number following the completion of the second division. Occasionally this separation does not come until after cleavage begins. Carnoy (1887a) reports such conditions in *Spiroptera strumosa*, where the reduced number of chromosomes of the sex cells (8) are further reduced to one-half (4). These chromosomes are dyad in structure, but become monad and double in number just before fertilization occurs. This gives the diploid number (16) for the zygote. *Filaroides mustelarum* (Carnoy, 1887a) also reduces from eight to four and then segments back to eight in each gamete, giving sixteen as the diploid number in the zygote. *Ascaris clavata* and an Ascarid of the dog (Carnoy, 1887b) both reduce to dyads in the germ cells and then separate during the cleavage divisions. Lukjanow (1889) reports a similiar condition of double reduction and secondary separation in *Ascaris marginata*. McDowell (1906) and Schleip (1912) while working on *Angiostomum nigrovenosum* found an intermediate condition in which the pairing might or might not occur during Prophase I, giving either twelve dyads or six tetrads to reduce to six monads. The second pairing was found in the zygote where the six monads from each gamete united to form six dyads which later (oogonia and spermatogonia) divided into twelve monads. The soma cells showed monad chromosomes after their first division. Similar pairings of the haploid number has been described for various other animals besides the Nematodes: Birds (Guinea and Chicken — Guyer, 1909a, 1916; Pigeons — Guyer, 1900, Smith, 1912); Mammals (Man — Guyer, 1910, and others; Opossum — Jordan, 1911; Horse, Pig, Mule, Cattle — Wodsedalek, 1913, 1914, 1920; Mongoose — Jordan, 1916); Lepidoptera (Seiler, 1913); and Hymenoptera (*Osmia cornuta* — Armbruster, 1913; *Apis mellifica* — Nachtsheim, 1913). In *Gallus* and *Phragmatobia* the secondary pairs break down in Prophase II; in *Apis mellifica*, and probably in most of the other cases, they do so before zygote formation is completed.

(2). There is a fusion of the chromosomes in the cleavage nucleus to less than the theoretical diploid number. Italis often shows such a condition, particularly in some strains (Taylor, 1917), and Carnoy

(1887 b) showed that a similar condition obtained in *Ascaris clavata* where the zygote carried sixteen chromosomes and the embryonic soma cells only twelve. Cutler (1918) found a condition in pheasants in which the fusion varied greatly, cells having anywhere from one to eight less chromosomes than the diploid number of twenty-two.

The present writer is inclined to interpret these cases — basing this upon intensive work on the di-tetrad chromosomes of various of the Nematodes — as indications of the physiological grouping of oocytic and spermatocytic chromosomes into compound forms which are essentially tetravalent, and reduce to a univalent condition in the mature ovum and spermatozoon. The "biseriale Anordnung" of Häcker (1895), well illustrated among the Copepods and some of the Cyclops (Braun, 1909; Matscheck, 1910; Krimmel, 1910; and Kornhauser, 1915), is brought to a climax by the actual union of the two portions into one before the maturation division occurs. Dyads would be formed by such a union of homologous monads. The first step would bethe formation of compound chromosomes as in *Ancyracanthus*, which do not retain their duplex condition for the entire germ cycle. In forms with "diminuted" soma cells, the next step is the formation of compound chromosomes in the germ cells. A third phase would entail the presence of compound chromosomes in all of the embryonic cells. Such cells, undergoing pseudo-reduction, would form tetrads, since the simplest morphological combination would be at least dyad in form. A further indication of a physiological compactness of the germ cell chromosomes is indicated by the double reduction, one in each of the two maturation prophases (Mongoose etc). The chromosomes of Prophase I are physiologically eight-parted, but as yet physically only four-parted, the second fusion occuring later. The next phylogenetic step is found in the actual physical as well as physiological formation of the eight-parted, or di-tetrad chromosomes of Prophase I of Sycon sponges, *Ascaris mystax*, *Ascaris canis* etc. That such a process could conceivably be carried much further is shown in the case of *Ascaris megalocephala univalens*, where the somatic number of chromosomes — seventy-two — has been reduced by fusion to a single compound chromosome in the matured germ cells.

It is the purpose of the writer in this paper to attempt to throw further light on the questions which have been so briefly summarized above, and to attempt to combat or confirm some of the discussed theories by a broadly comparative study of considerable Nematode material.

The following table (Table I) is an attempt to collect the available information concerning the diploid and haploid chromosome numbers of the parasitic Nematodes. The somatic number and the composition

Table I.

Name	Haploid number	Diploid number	Somatic number	Heterochromosome	Authority
Ascaris canis	18	30—36	60—72	X = 6	Walton, 1916a, 1918
Ascaris clavata	12	24	48	?	Carnoy, 1887 b
Ascaris felis	9	18	?	X = 1	
				Y = 1	Edwards, 1911
	9	18	36	[1] X = 1	Boveri, 1911
					Walton, 1916a, 1921
Ascaris incurva	21	35—42	35—42	X = 8	
				Y = 1	Goodrich, 1916
Ascaris labiata	?	?	diminution	?	Meyer, 1895
Ascaris lumbricoides	24	43—48	?	X = 5	Edwards, 1910
			43—48		Bonnevie, 1902
Ascaris marginata	11	22	22	?	Kultschitzky 1888
Ascaris megalocephala univalens	1	2	47—48	[1] X = 1	Boveri, 1909 b
			52—60	[1] X = 8	Geinitz, 1915
			63—72	[1] X = 9	Kautsch, 1913
Ascaris megalocephala bivalens	2	4	?	[1] X = 1	Boveri, 1909 b
			62—70	[1] X = 8	Guieysse. Pellissier, 1909
			135—144	[1] X = 9	Kautsch, 1913
Ascaris megalocephala trivalens	3	6	?	?	Zacharias, 1912
Ascaris mystax	11	22	44	X = 1, Y = 1 ?	Marcus, 1906
Ascaris rubicunda	?	?	diminution	?	Meyer, 1895
Ascaris sp.? (from dog.)	4	8	16	?	Carnoy, 1887 b
Angiostomum nigrovenosum	6	11—12	22—24	X = 1	Boveri, 1911
				X = 1, [2] Y = 1	Schleip, 1911
Ancyracanthus cystidicola	6	11—12	11—12	X = 1	Mulsow, 1912
Cornilla robusta	8	16	8	?	Carnoy, 1887 a
Filaria papillosa	6	11—12	11—12	X = 1	Meves, 1915
Filaroides mustelarum	8	16	16	?	Carnoy, 1887 a
Heterakis dispar	5	9—10	9—10	X = 1	Gulick, 1911
Heterakis inflexa	5	9—10	9—10	X = 1	Gulick, 1911
Heterakis vesicularis	5	9—10	9—10	X = 1	Gulick, 1911
Heterakis sp.? (from pheasant)	5	9—10	9—10	X = 1	Boveri, 1911
Ophistomum mucronatum	6	12	24	?	Carnoy, 1887 a
Oxyuris ambigua	4	7—8	7—8	X = 1	Meves, 1921
Rhabditis aberrans					
(female-parthenogenetic)	9	18	18		
(male-non-functional)	8+X×Y	18	18	X = 1, [2] Y = 1 ?	Krüger, 1913
Rhabditis aspera	7	13—14	13—14	X = 1	Kröning, 1923
Rhabditis pellio Bütschli	7	13—14	13—14	X = 1	Kröning, 1923
Rhabditis pellio Schneider	7	13—14	13—14	X = 1	Kröning, 1923
Sclerostomum edentatum	6	11—12	11—12	X = 1	Kühtz, 1913
Sclerostomum equinum	6	11—12	11—12	X = 1	Kühtz, 1913
Spiroptera strumosa	8	16	12	?	Carnoy, 1887 b
Strongylus filaria	6	12	12	X = 1, Y = 1 ?	Struckman, 1905
Strongylus paradoxus	6	11—12	11—12	X = 1	Kröning, 1923 Gulick, 1911
Strongylus micrurus	6	11—12	11—12	X = 1	Krönin g, 1923
Strongylus tenuis	6	11—12	11—12	X = 1	Gulick 1911
Strongylus tetracanthus	6	12	12	?	Meyer, 1895

[1] Heterochromosome commonly attached to end of an autosome.
[2] Y chromosome lost during the metamorphosis of the spermatid.

of the heterochromosome group when present, is also included for such forms as could be located. No attempt has been made to include the free-living or plant-inhabiting Nematodes, or any of the Gordiacea and Acanthocephali.

III. Materials and Methods.

The material was all obtained in the living condition and immediately preserved. The smaller forms were killed and fixed *in toto* while the larger forms had the germinal elements dissected out in warm physiological salt solution and then killed and fixed. FLEMMING's fluid (strong), BOUIN's fluid, PETRUNKEVITCH's modification of GILSON's fluid, CARNOY's fluid, Glycerine and Alcohol, and 5% formol were used as fixation agents. The most favorable results were obtained following fixation in PETRUNKEVITCH's, BOUIN's and CARNOY's fluids, the first being especially valuable in the case of eggs and embryos.

The best sections were obtained from material embedded in paraffin by the benzol-chloroform method. Those cut varied from 4 μ to 15 μ in thickness, with the best results from the thinner sections. HEIDENHAIN's iron-alum-haematoxylin or DOBELL-KUDO's modification of alcoholic iron-haematin, followed by a counterstain of Bordeaux red or Orange G, was the staining method usually employed. Safraninlicht grün, alizarin-krystal violet, and EHRLICH-BIONDI stains were also used for comparative work, but not found satisfactory. SCHNEIDERS acid carmine was used in the study of crushed mounts and smear preparations to determine the stages of maturation before embedding and sectioning the germinal tubes of the larger forms.

The new fluid — CARNOY Phenol (HETHERINGTON, 1922) — was found to give excellent results in the preparation of whole mounts for the purpose of identification of species, but did not lend itself readily to the making of sections as most stains do not follow its use without losing much of their sharply specific differentiations. As a short cut to embedding, its use after any of the other fixation agents is a very great time saver, and apparently short immersions in it has no effect upon the stainability of the tissues so treated.

IV. Experimental evidences.

The studies to be recorded in this paper were based upon material obtained from a variety of hosts and comprises sixteen species, representing twelve genera, ten sub-families, eight families and five superfamilies of the order Nematoda. The complete list is as follows: (See Table II):

Table II.

Order	Super-family	Family	Sub-family	Genus	Species
Nematoda	*Ascaroidea*	*Ascaridae*	*Anisakinae*	*Contracaecum*	*spiculigerum*
			Ascarinae	*Ascaris*	*lumbricoides*
					megalocephala biv.
					megalocephala univ.
				Belascaris	*mystax*
					triquetra
				Toxascaris	*canis*
		Heterakidae	*Heterakinae*	*Gangulaterakis*	*spumosa*
				Heterakis	*papillosa*
	Filaroidea	*Acuariidae*	*Acuariinae*	*Acuaria*	*spiralis*
		Spiruridae	*Physaloptera-inae*	*Physaloptera*	*turgida*
			Spirurinae	*Protospirura*	*muris*
	Oxyuroidea	*Cruxidae*	*Cruxiinae*	*Cruxia*	*tentaculata*
		Oxyuridae	*Oxyurinae*	*Syphacia*	*obvelata*
	Strongyloidea	*Trichostrongylidae*	*Heligmosominae*	*Nematospira*	*turgida*
	Trichinelloidea	*Trichinellidae*	*Trichosomoidinae*	*Trichosomoides*	*crassicauda*

A. Ascaroidea.

1. Ascaridae.

Anisakinae.

a) *Contracaecum spiculigerum* (Rud.) Railliet & Henry. From the pouch, esophagus and stomach of the white pelican — *Pelecanus erythrorhynchus.*

Syn. *Ascaris spiculigerum* Rud.

The material was collected at Yellowstone National Park during the breeding season of the birds, and has become available for this study through the courtesy of Dr. Ward.

Study of the spermatogonia shows that there are fifteen small rod-shaped chromosomes, some of which show a slight transverse constriction near the middle which probably indicates the position of the Querkerbe (Walton, 1918). During interkinetic periods the spermatogonial chromatin is gathered into a single large karyosome which later gives rise to all of the chromosomes. During the growth period which follows the last spermatogonial division, the chromatic material does not assume the form of a large clump, but breaks up into fine "chromioles" which become entangled in the intersticies of the reticular ground substance of the nucleus. A large plasmosome is usually present, situated cen-

trally within the nucleus. Toward the end of this period, the haploid number of chromosomes — eight — are segregated out from the reticulum. Each of these shows a definite transverse constriction (fig. 1). Shortly before the chromosomes enter the metaphase plate they show a very definite longitudinal striation and faint indications of a second such marking is noted in seven of these bodies. The metaphase plate of the primary spermatocyte receives seven di-tetrad and one tetrad chromosomes (fig. 2), the latter being the heterochromosome.

The first division is clearly longitudinal, each daughter chromosome showing the Querkerbe distinctly. Each chromosome is attached to a definite group of mantle fibers, giving a banded appearance to the spindle. The chromosomes separate first at the end to which the fibers are attached and appear "V" shaped for a short period before the opposite end finally parts from its synaptic mate. The anaphase spindle shows the heterochromosome lagging behind the autosomes in its passage to one pole. Two classes of daughter cells are thus formed, one with seven and the other with eight chromosomes. All of the chromosomes show a definite cross-constriction — the Querkerbe — as well as a longitudinal cleft, thus being tetrad in composition.

Metaphase plates (fig. 3, 4) of the secondary spermatocytes show that the tetrad chromosomes are so arranged that the second division will again be longitudinal, reducing them to dyads in the spermatids (fig. 5). During the metamorphosis of the spermatid into the spermatozoon, the chromatic material becomes clumped into a single saucer-shaped mass which gradually assumes a spherical condition in the matured spermatozoon (fig. 6, 7, 8).

As is commonly the case in most Nematodes, the maturing male germ cells contain a large number of "refringent corpuscles" which in the spermatogonia are irregularly scattered throughout the cytoplasm, each granule containing one or more mitochondrial bodies. During the meiotic process the granules become ovoid in shape and assume positions in rows radiating outward from the centrosomes in a manner resembling the spokes of a wheel. Besides the mitochrondria, the granules contain two other types of material; one a framework or ground substance built up about certain granules of nuclear origin, and the other of nutritive substance which has been elaborated from the cytoplasm by the activity of this nuclear material and stored around it. In *Ascaris megalocephala* and *A. canis* (*Toxascaris*) it has been shown by earlier work that during metamorphosis the mitochondria leave the granules and form a polar cap around one side of the nucleus. The refringent bodies then assume a peripheral position in the spermatids, gradually coalescing and migrating to what might be called the tail of the amoeboid spermatozoon. This body is now called the "residual body", or "Glanz-

körperchen", and acts as a reservoir of nutritive material upon which the spermatozoon depends during the long period between its formation and the time of insemination. The longer the intervening period, the greater the reduction of this nutritive material. The reduction may occur either from the center outwards or from the surface inwards, the end result being the same in either event. If insemination has failed to occur by the time the "Glanzkörper" is entirely exhausted, the spermatozoa lose their viability and shortly degenerate. The size of the nutritive body is therefore a definite criterion for the age of the spermatozoon and also indicates the approximate length of time between copulation and insemination. Some spermatozoa fail to develop any such reserve material — *Acuaria spiralis, vide infra* — at any period of their existence, and in such cases it is usually found that copulation between sexes is often and that the seminal vesicle is large while the seminal recepticle is small, indicating that the spermatozoa spend but a short time in the body of the female before accomplishing their purpose or becoming useless and quickly degenerating to give place to the next batch of fresh spermatozoa.

In *Contracaecum spiculigerum* the process by which the "refringent granules" of the spermatocytes are eliminated from the spermatid and resulting in the so-called "cytophore" formation has been worked out in detail. The refringent granules give up their contained mitochondrial bodies in the usual manner in the spermatids. The nutritive material of the granules then migrates to the periphery of the cell (fig. 5), coalesces, and forms a definite, continuous, superficially placed layer to the cytoplasm. The reticular ground substance of each granule retains its original position, giving a very faintly staining radiating appearance to the cytoplasm of the spermatids. This network breaks down and no trace of it is found in the matured spermatozoon. The peripheral layer of heavily staining nutritive material — glycogen according to Marcus, 1906 — diffuses out through the cell wall and forms in small droplets just outside of the membrane (fig. 6). These gather into larger masses — cytophores — and are found scattered in small groups throughout the spermatozoa (fig. 7), finally being pushed to the walls of the seminal vesicle where they undergo complete degeneration with no further functioning. The spermatozoa do not assume the amoeboid shape until after copulation has occurred and they are in the seminal receptacle of the female. No trace of any Glanzkörperchen is found, and the spermatozoa soon lose their viability and degenerate unless insemination is immediate. The structure of the female is in agreement with this adaptation on the part of the male germ cells in that there is a very small seminal receptacle and hence no room for the storage of surplus spermatozoa as would be necessary if fertilization were a

long drawn out process in which they were furnished to the slowly maturing eggs as these became available.

Study of the oogonia shows the presence of sixteen small rod-shaped chromosomes which arise from a single karyosome present in the interkinetic periods. After the last oogonial division, these sixteen chromosomes enter a spireme condition out of which develop eight haploid chromosomes, each possessing a definite Querkerbe (fig. 9). Before entering the metaphase plate of the first maturation division, each chromosome develops two longitudinal splits at right angles to each other. One represents the plane of syndesis and the other the longitudinal split of the diploid chromosome before it becomes haploid by parasynapsis. The metaphase chromosome (fig. 10) is therefore a ditetrad.

The first division is longitudinal, each daughter plate receiving eight tetrad chromosomes (fig. 11). The second division is likewise longitudinal and the ootid is left with eight dyad chromosomes in its nucleus (fig. 12). The female pronuclei when organized, contain eight dyad chromosomes each, and the two types of male pronuclei have seven and eight respectively. The fusion nucleus of the male-producing zygote contain fifteen dyad chromosomes and that of the female-producing zygote, sixteen.

Examination of larvae shows that the propagation cells and soma cells both retain these characteristic numbers of diploid chromosomes throughout their life cycle. Somatic nuclei of the adult worms also show these same numbers. In no case was a reduction to a monad condition accompanied by doubling of the numbers of chromosomes observed. The Querkerbe may represent a point of former union — i. e., phylogenetically — of two monad somatic chromosomes, but in this worm that union has become permanent through the entire life cycle of both the germinal and the somatic cells. No evidences of the occurrence of a diminution division were obtained.

The gametogenesis of *Caontracecum spiculigerum* shows that the diploid number of chromosomes is fifteen for the males and sixteen for the females, reducing to seven and eight, and eight respectively, for the haploid numbers. The meiotic chromosomes are di-tetrads which reduce through two divisions to a dyad-like structure in the mature germ cells. The heterochromosome is of the X type and passes undivided to one of the two daughter cells of the first maturation division. There is no evidence that the heterochromosome exists as a separate body during interkinesis or that it arises from a separate karyosome after the growth period of the primary spermatocytes is completed. There is no difference in number or structure between the chromosomes of the germ cells and those of the somatic cells. A diminution division does not occur. The eggs contain well developed larvae at the time

of laying, and are deposited in large numbers at any one time. Copulation and immediate insemination is periodic and occurs soon after the female has deposited a large batch of eggs. Insemination occurs between the first and second maturation divisions of the egg.

Ascarinae.

a) *Ascaris lumbricoides* Linn. Small intestines of the pig, occasionally in man.

Boveri (1887), Carnoy (1887 a), Fürst (1898), Bonnevie (1902) and Edwards (1910 b) have made careful studies of the germ cycle of *A. lumbricoides*, determining the haploid number of chromosomes to be twenty-four in the egg (Boveri, Carnoy, Fürst and Bonnevie), and nineteen or twenty-four in the spermatozoa (Edwards); the diploid number as forty-eight to fifty (Bonnevie); and the somatic number as forty-eight to fifty. A diminution division takes place, beginning with the division of the four-celled stage. In such a division the two ends of each rod-like chromosome are cut off and lost from the spindle while the central portion remains intact as the somatic chromosome.

Recent studies of a large amount of fresh material has corroborated in all major aspects the results of the workers quoted above. In addition, a certain number of facts have brought themselves to the attention of the writer and forced him to regard *A. lmbricoides* as worthy of renewed consideration at the present time. Edwards (1910 b) figures (pl. 22. fig. 24-25) the reduced number of spermatocytic chromosomes as twenty-four, of which nineteen are bivalent and five are univalent. Theoretically these are tetrads and dyads respectively, inasmuch as each autosome undergoes two maturation divisions — only one of which can take place along the plane of syndesis, the other being equational—, and each heterochromosome one division — which is also equational. Detailed examination of a large number of nuclei, both male and female, has resulted in the finding of a few individuals in which the plane of the equational division is indicated beforehand by an external constriction which lies at right angles to the plane of syndesis. Owing to the change of shape of the chromosomes while preparing for the first division, this second plane of future division appears to be transverse, although actually it is longitudinal at the time of its formation. Both divisions are therefore longitudinal. Edwards describes one of the members of the X group as being often larger than the others, and apparently showing an attachment to the autosomes (pl. 22. fig. 30). In several cases the writer has found instances of the consistant appearance of a larger member in all of the heterochromosome groups within a single nematode, and in such material, the heterochromosome group always is preceeded along its pathway to one or the other of the poles

of the first division by this larger chromosome. This element is attached by fibers to the autosomes in a manner similar to that reported for *Contracaecum incurvum* (Goodrich, 1916, pl. 3 fig. 38-43). The oocytes also show in a large number of cases one tetrad which is larger than any of the others, and which probably represents the 2 X condition of the large element in the X group of the male. All chromosomes of the second maturation stages show as dyads, and reduce to monads in the spermatids and the ova. There is a distinct size dimorphism of the nuclei among the spermatozoa. The fusion nucleus shows forty-three or forty-eight monad chromosomes, according to the number — nineteen or twenty-four — in the fertilizing spermatozoon.

Bonnevie (1902) made a careful study of the diminution phenomenon in *A. lumbricoides* and determined that forty-eight to fifty chromosomes remained after ninety-six to one hundred chromatic granules were cast off and lost (pl. 16 fig. 11—13). Examination of segmenting eggs showed that there is a sexual difference in the chromosome numbers of the soma cells (fig. 13—14). Cells in any one embryo show either forty-three or forty-eight chromosomes after diminution.

Ascaris lumbricoides furnishes an example of a form in which the gametic chromosomes are compound, each one consisiting of three parts, one of which is retained in the somatic cells, and two of which are cast off from the nucleus and degenerate in the cytoplasm. The haploid chromosomes have the morphological aspect of tetrads.

b) *Ascaris megalocephala* Cloquet. Small intestines of the horse.

The results included here are based upon a series of observations on material from a considerable number of sources that have become available from time to time during the past six years, and includes examples of both *Ascaris megalocephala bivalens* and *A. megalocephala univalens*. The examination of the materials was largely with the purpose of detecting instances of the separate existence of the heterochromosome, and also of determining the constancy of numbers among the chromosomes of the soma cells after diminution had taken place.

The investigations of Boveri (1899, 1909 b), Boring (1909), Frolowa (1912 b), Zacharias (1913), Kautzsch (1913) and Geinitz (1915) have established rather definitely the fact of the presence of a single X chromosome in the males, and two X chromosomes in the females of both varietie of *A. megalocephala*. These workers report that only approximately five per cent of the worms examined show the heterochromosomes as being unattached to the autosomes, and when so isolated, a detectable shortening of one or more of the autosomes is present. Several investigators have reported that the reduction division occurs during Metaphase I (Edwards, 1910b, *et alii*), but that occasionally

failures to divide occur, and in such cases the reduction comes at the time of the second division. Geinitz (1915) made a careful study of such conditions as found in the oocytes of *A. meg. biv.*, and reported that the division process is very irregular. In many eggs only one heterochromosome is identifiable, in others, both are recognizable. As a result of the irregularities in division, some mature ova contain two, some one, and some neither of the heterochromosomes.

Several estimations of the number of somatic chromosomes present after diminution have been made by various workers. For *A. meg. univ.*, Boveri (1909 b) reports embryos showing forty-seven and forty-eight somatic chromosomes, the difference being sexual, with X equaling one. Kautzsch (1913) found sixty-three and seventy-two, with X equaling nine. Each germinal autosome is a complex of twenty-seven somatic chromosomes. Geinitz (1915) finds that X equals eight, and that the somatic numbers are fifty-two and sixty. Each autosome is made up of twenty-six somatic chromosomes plus the amount lost at diminution. For *A. meg. biv.*, Boveri (1909 b) finds X equals one, but gives no number of somatic chromosomes. Guieysse-Pellissier (1909) thinks that X equals eight, and that the somatic number of chromosomes is sixty-two and seventy. Kautzsch (1913) maintains that X equals nine, each autosome equals twenty-seven, and leaves the reader to infer that the somatic numbers are one-hundred and thirty-five and one hundred and forty-four, although he makes no definite statement as to those figures.

The present observations have led the writer to the conclusion that the heterochromosome is of the X type, and is attached to the end of an autosome in approximately ninety per-cent of the cases in both males and females. In the males the X chromosome consistantly undergoes reduction at the time of the first division, both in *A. meg. univ.* and *A. meg. biv.* No such regularity of the time of reduction was observed in the case of oogenesis. However, about seventy-five per-cent of the number of cells examined showed the mature ova with only one X, the reduction occuring in more than sixty per-cent of these instances at the time of the first maturation division. The numbers were about equal in which the ova either failed to contain either heterochromosome, or else contained both. No instances were considered in which a check could not be made by referring to the polar bodies and determining the presence or absence of the heterochromosome there. Two cases were observed in which the X chromosomes were lost out of the spindle and remained in the cytoplasm some distance from the nuclear area. Geinitz (1915, pl. 40, fig. 64, 68) has figured similar conditions observed in *A. meg. biv.*

Numerous counts were made of somatic cell chromosomes, and the average results point to the presence of twenty-six chromosomes for

each autosome of *A. meg. univ.*, with X equaling eight. This substantiates the results of GEINITZ (1915). Careful counts of material from *A. meg. biv.* showed that each autosome was equivalent to twenty-two or twenty-three somatic chromosomes, and X equals eight. The somatic number would then approximate eighty-eight to one-hundred, with the sexual difference of eight in each case. This agrees with the fact that careful measurements have shown that the chromosomes of *A. meg. biv.* are slightly smaller than those of *A. meg. univ.*; they should be smaller having less chromatic material per chromosome.

A. meg. univ. affords the extreme example of the complexity of the germinal chromosomes in possessing a single gametic chromosome which is equivalent to twenty-six somatic chromosomes, plus the amount of chromatin lost by diminution, and, in the case where the X elements are united to the autosome, the gametic chromosome contains eight additional heterochromosomal elements. The haploid chromosomes have the morphological appearance of tetrads, although equivalent to at least twenty-six somatic chromosomes. According to BLANCKERTZ (1910) these autosomes are resolvable with careful observation into twelve elements, each of which if double would account for twenty-four of the minimum number found in the soma cells. No other observer has been able to substantiate this report, so the germinal chromosomes are still regarded as tetrads at the beginning of the maturation divisions.

c) *Belascaris mystax* (Zed.) Castellani & Chalmers. Small intestines of cats.

Syn. *Ascaris cati* Schrank
Ascaris felis Gmelin
Ascaris mystax (Zed.) Rudolphi
Ascaris mystax felis (Gmel.) Railliet.
Ascaris terers Goeze
Fusaria mystax Zeder
Lumbricus teres intestinalis Linn.

In 1911 EDWARDS made a brief cytological study of *Ascaris felis*, establishing the fact that a heterochromosome complex was present. This complex he interpreted as an X — Y pair, in which the X element was twice as large as the Y. BOVERI, in a foot-note to the paper by EDWARDS, favored the interpretation that the sex chromosome was of the single X type, attached to the end of an autosome in a manner similar to that reported for *Ascaris megalocephala*. WALTON (1921) working on the spermatogenesis of *A. felis* came to the conclusion that his material afforded evidence that favored the interpretation of BOVERI — there is a single X chromosome present which typically is attached to the end of one of the autosomes, but which occasionally was separated and could be traced as an independent unit throughout meiosis.

The present work is a review of the conditions found in the male sex cells, and a study of those found in oogenesis; conditions in the latter having been predicted by EDWARDS (1911) but as yet no definite report on them has appeared.

Study of spermatogenesis has shown the following:

1. *B. mystax* shows nine chromosomes for the haploid number, eight tetrad autosomes, and one hexad heterochromosome which consists of a dyad idiochromosome attached to the end of one of the autosomes.

2. This union occurs in the primary spermatocytes, the idiochromosome being a separate chromatic entity in the spermatogonia.

3. The idiochromosome is of the X type, undergoing quantitative division at the time of the formation of the spermatids.

EDWARDS (1911, p. 311) gives the following formula for sex-production in *Belascaris mystax* based upon his interpretation of the structures present in the male.

a) Egg X + Spermatozoon X = XX (Female).

b) Egg X + Spermatozoon Y = X Y (Male).

Supplying the numbers, the formula would then read:

a) Egg (8 + X) + Spermatozoon (8 + X) = 16 + 2 X or 18 (Female).

b) Egg (8 + X) + Spermatozoon (8 + Y) = 16 + X + Y or 18 (Male).

In such a case the diploid number should be eighteen univalent chromosomes for each sex, and the haploid, nine bivalents; X and Y forming the ninth bivalent. Based upon the results as interpreted from the results obtained by the writer (WALTON, 1921) in his study of the spermatogenesis of *B. mystax*, the formula as given for the egg by EDWARDS would hold, but not that for the sperm. Substitution of chromosome numbers in the formula for the egg would, however, change its value.

a) Egg X + Spermatozoon X = XX (Female). (9 + X) + (9 + X) = 18 + 2 X (Female).

b) Egg X + Spermatozoon = X (Male). (9 + X) + (9) = 18 + X (Male).

In both cases the X is normally attached to the end of an autosome so that the diploid number in eighteen and the haploid nine, although the potential numbers are twenty and nineteen. In the male eight of the diploid chromosomes are tetrad and the ninth is hexad in structure.

With this predicted condition in view, a careful study of oogenesis has been carried out with the following results.

The oogonia, as is characteristic of those of the other ascarids, show several unequal karyosomes and one or more plasmosomes which disappear during the growth period. Counts of oogonial chromosomes were fairly easy to obtain, and showed eighteen to twenty in every case. Based upon conditions observed during the study of spermatogenesis, the occasional isolated condition of the heterochromosome is

not unknown, so that it seems not at all improbable to interpret a condition of nineteen or twenty chromosomes as indicating that one or both of the idiochromosomes were free from any attachment to an autosome. The chromosomes were so minute that no size dimorphism was discernible in the cases where the idiochromosomes were attached to autosomes.

Toward the end of the growth period, the chromatic material of the nucleus is gathered in a large, densely staining peripheral mass, closely enmeshed in a network of linin threads. Typically eighteen centers of chromatic aggregations, occasionally nineteen or twenty, are formed, and around these are laid down the prophase chromosomes, two of which are larger and show a transverse constriction at about one-third of their length (fig. 15). These chromosomes immediately reduce by parasyndesis to nine, each showing a double longitudinal split, thus being tetrad in structure. One of these is larger than the others and represents the tetrad autosome with a tetrad idiochromosome attached to one end. This chromosome is essentially a very unequally divided di-tetrad. The first division reduces the autosome pairs to dyads as well as the heterochromosome, leaving the secondary oocytes with eight dyad chromosomes and one tetrad (fig. 16). The second division is entirely regular, each chromosome dividing longitudinally, leaving eight monad autosomes and one dyad heterochromosome.

This chromosome consists of a monad autosome and a monad idiochromosome attached end to end. At the time of fertilization, the female pronuclei all show the nine chromosomes (9 + X) while the two types of male pronuclei show also nine, but of two values (9 + X and 9). (Fig. 17—18.)

The fusion nucleus (fig. 19—20) gives two different appearances, each with eighteen chromosomes, but in one case two of these are larger than the others, while in the second instance only one chromosome is larger than its mates. These large chromosomes consist of an autosome and its attached idiochromosome.

There is a diminution division similar to that found in *Ascaris canis* (Walton, 1918) i. e., beginning with the second or third cleavage and ending with the sixth. The soma cells all show eighteen chromosomes (fig. 21), similar in appearance to those in the germ cells, but somewhat smaller due to the loss of a portion of their substance at the time of the diminution division.

Study of the oogenesis of *Belascaris mystax* shows the expected 2 X condition of the sex-chromosome. The diploid number of chromosomes is eighteen and the haploid nine. The idiochromosome is consistantly attached to the end of one of the autosomes. *B. mystax* does not show the presence of compound chromosomes in the germ cells, since the

number in the somatic cells after diminution is the same as that in the germ cells. The chromatin lost into the cytoplasm at that time is probably, as in all other instances where it occurs, simply a fragmentation process, not a splitting of a complex body into its componant parts.

d) *Belascaris triquetra* (Schrank) Leiper. Small intestines of wolves, bears and occasionally dogs.

Syn: *Ascaris canis* (Wer.) Gmelin,
Ascaris marginata Rudolphi,
Ascaris mystax (Zed.) Rudolphi,
Ascaris teres (*vulpis*) Goeze,
Ascaris triquetra Schrank
Ascaris vulpis Froelich,
Belascaris vulpis (Froel.) Railliet & Henry,
Fusaria triquetra (Schrank) Zeder,
Toxascaris limbata Railliet & Henry.
Toxascaris marginata (Rud. and Leiper) Railliet & Henry,

In 1888 KULTSCHITZKY found twenty-two diploid chromosomes in a study of the oogenesis of *Ascaris marginata* Rud. These reduced by the maturation division to eleven. LUKJANOW (1889) also worked on what he called *A. marginata*, but recent work has cast considerable doubt as to the validity of his identification. MARCUS (1906) worked on material he believed to be *A. canis* Werner (sp. *mystax*), but later investigations (EDWARDS, 1911; WALTON, 1916a, 1916b, 1918) have shown that his material was not *A. canis* (*Toxascaris canis*) but most probably *A. triquetra* Schrank (*Belascaris triquetra*). MARCUS reported that the unreduced number of chromosomes in his material was twenty-two, thus corroborating the results of KULTSCHITZKY. Undoubtedly the two investigators worked upon the same form. MARCUS further showed that twenty of these chromosomes were paired, and two unpaired, so that each primary oocyte and spermatocyte had ten bivalent and two univalent chromosomes. The first division showed that two univalents passed undivided, one to each of the daughter nuclei. Each daughter nucleus thus received eleven univalent chromosomes.

After passing through a spireme stage, the prophase chromosomes were formed, showing distinct "end-to-end" halves. Each half consisted of a single tetrad mass, formed by two longitudinal splits at right angles to each other. The haploid chromosomes were therefore octads, formed by telosyndesis of two tetrads. The second maturation division was reductional.

The first segmentation nucleus showed twenty-two dyad chromosomes which fused into eleven tetrads in each of the daughter nuclei. Diminution occured in the first division of the primary soma cell, and

in each soma cell thereafter formed from the propagation cell. The germ cells become isolated at the time of the sixth cleavage of the embryo. After the diminution all of the soma cells show twenty dyad chromosomes while the germ cells still possess eleven tetrads.

In order to confirm or combat the supposition that MARCUS actually studied *A. triquetra* under the name of *A. canis* (*mystax*), and to check definitely upon his results as well as to clear up questions concerning the cytological condition of gametogenesis in *Belascaris triquetra* (Schrank) Leiper, the writer has made a careful study of both spermatogenesis and oogenesis in that species.

The material used was obtained from worms collected from the intestines of a dog killed at Cambridge, Mass., and careful identification was made at Harvard University.

As is the case with *B. mystax*, the spermatogonia of *B. triquetra* are very small, and the nuclear material tends to clump to such an extent that chromosomal counts are very difficult. The number does not seem to exceed twenty in the majority of the counts obtainable. Examination of nuclei in the resting stage showed the presence of two small plasmosomes and two very unequal karyosomes.

The chromatin of the growing spermatocytes appears in the form of two irregular masses located peripherally in the nucleus, one of which is very much smaller than the other. A distinct plasmosome is also present during this period. The karyosomes become connected to the superficial network of linin fibers. Soon after becoming a part of this network, the two chromatin bodies show a segregation of their chromatic material into discrete bodies embedded in a heavy meshwork of linin. The larger of the two chromatic masses gives rise to twenty of these small centers of chromatin aggregation, while the smaller mass gives rise to but two (fig. 22). The minute chromatin clumps assume the form of definite chromosomes as the linin background disappears. The twenty chromosomes all assume a tetrad condition by the appearence of a longitudinal split and a cross-constriction or Querkerbe. Following a synaptic period, twelve chromosomes are found, ten of which are di-tetrads, formed by parasyndesis of the twenty tetrads originating from the larger chromatic mass of the early growth period. The two tetrads — the heterochromosomes — which developed from the smaller chromatic mass, do not pair, and appear as tetrads in the late prophase. The metaphase plates thus contain ten di-tetrads and two tetrads. The first division divides each of the ten di-tetrads — autosomes — longitudinally but fails to affect the heterochromosomes, although they delay considerably before following the autosomes to one pole.

Two kinds of second spermatocytes are thus formed, one containing ten tetrad chromosomes and the other ten tetrad autosomes and two

tetrad heterochromosomes (fig. 23-24). In the second division all of the chromosomes are divided, although the heterochromosomes are delayed in their action and lag behind in their progress toward the poles. Two kinds of spermatids are formed, one with twelve dyad chromosomes and one with ten (fig. 25-26). After the clumping of the chromosomes in the spermatozoon nucleus, no measurable differences in size of the two types were detectable, probably as the difference in chromatic content is very small.

The male of *B. triquetra* thus contains twenty-two dyad chromosomes for the diploid number which reduces to ten di-tetrads and two tetrads as the haploid group. The heterochromosomes are of the X type, the group consisting of two members which undergo equational division in the second maturation spindle. These heterochromosomes are segregated from a karyosome which has had a separate existence during the spermatogonial stage as well as in the early period of the primary spermatocyte. The spermatogonial chromosomes are compound, showing a dyad structure when first recognizable.

As is the case with the spermatogonia, the oogonia are very difficult to study because of their small size, but careful observation enables one to count about twenty chromosomes in the metaphase plates. Primary oocytes show twenty-four dyad chromosomes during the growth period. Just before the end of the growth period, the chromosomes lose their definite outlines and become diffused throughout the nucleus. Following this stage, two very unequal karyosomes are formed, and from these crystallize out twenty-four chromosomes (fig. 27) which immediately show both the Querkerbe and a longitudinal split (fig. 28). The peculiar formation of these chromosomes is rather striking. As in the primary spermatocytes, the first oocytes show *two* karyosomes which later give rise to chromosomes. The peculiarity lies, not in the presence of two karyosomes — other animals show the same conditions —, but in the fact that from the smaller body are segregated four chromosomes and from the larger, twenty. These latter correspond undoubtedly to the autosomes of the male and the former are what are to be expected as representing the 2 X condition in the female, when X equals two, as it does in this species. That this stage is probably only of very short duration is shown by the fact that no corresponding presence of two unequal karyosomes, similar to those in the spermatogonia, is found in the oogonia.

The twenty-four oocytic chromosomes are reduced though a process of parasyndesis the their haploid condition — twelve di-tetrads. Metaphase plates (fig. 29—30) show twelve di-tetrad chromosomes, all of which undergo equal division, leaving twelve tetrads to form the metaphase plate of the second oocyte (fig. 31). Anaphase plates

show that a second longitudinal division has occured, leaving twelve diad chromosomes in the egg to form the female pronucleus. Eggs containing both pronuclei showed that the fertilizing spermatozoon nucleus containede ither ten or twelve diad chromosomes while each female pronucleus contained twelve. Study of the fusion nuclei showed that they contain either twenty-two or twenty-four dyad chromosomes.

Careful observation of the embryonic stages showed that a diminution process occurs which is very similar to that in *Toxascaris canis* (Walton, 1918). This division first occurs after the formation of the second soma cell, and results in the presence of two diminution figures as the same time (fig. 32). By this division, the somatic chromosomes are reduced to monads, forty-four or forty-eight in number (fig. 33). The somatic cells retain this increased number during at least the embryonic period, while the germinal cells retain the dyad condition. The propagation cells are definitely isolated at the end of the sixth cleavage.

The above results do not agree in their entirety with those of MARCUS (1906), but are very close, and agree in so many details that the writer believes that he is justified in assuming, at least from cytological grounds, that the material used by MARCUS was much more likely to have been *Belascaris triquetra* (Schrank) Leiper than *Ascaris canis* Werner (sp. *mystax*) as that investigator supposed it to be. The same argument holds for the material studied by KULTSCHITZKY (1888) as it seems well established that he studied the same species as did MARCUS.

The study of the oogenesis of *B. triquetra* Leiper affords the following facts: The diploid number is twenty-four dyad chromosomes, originating in the primary oocytes from the segmentation of two unequal karyosomes, and reducing by parasyndesis to a haploid condition of twelve di-tetrad chromosomes. A 2 X condition, where X equals two, is present. After fertilization is completed, the embryo contains twenty-two or twenty-four dyad chromosomes, which in the soma cells are increased to double the number found in the germ cells, and become monad in structure. The germinal chromosomes of *B. triquetra* are thu compound, and equivalent to at least two of the somatic chromosomes plus certain excess material which is lost into the cytoplasm at the time of the diminution phenomenon.

e) *Toxascaris canis* (Werner) Castellani and Chalmers. Small intestines of dogs.

Syn: *Ascaris alata* Bellingham,
Ascaris caniculae Schrank,
Ascaris caniculi Braun,
Ascaris canis (Wer). Gmelin,

Ascaris canis felis (Gmel.) Werner of Galli-Valerio,
Ascaris cati Schrank,
Ascaris felis Gmelin,
Ascaris marginata Rudolphi,
Ascaris mystax (Zed.) Rudolphi,
Ascaris teres (*canis*) Goeze,
Ascaris tricuspidata Brugiere,
Ascaris vulpis Froelich,
Ascaris werneri Rudolphi,
Belascaris canis (Wer.) Garin
Lumbricus canis Werner,
Toxascaris limbata Railliet & Henry
Toxocara canis (Wer.) Johnston,

A careful study of both spermatogenesis and oogenesis of this form has been made (Walton, 1916a, 1918) and as the results there were the bases upon which the present study was founded, a summary of those results may well be included at this point.

1. *T. canis* shows eighteen chromosomes for the haploid number, twelve di-tetrad autosomes and six tetrad heterochromosomes, the latter being of the X type.

2. There are two types of second spermatocytes and spermatids found, one type having twelve autosomes and six heterochromosomes, the other having but the twelve autosomes.

3. The diploid number of chromosomes is thirty-six; the haploid number for the female is eighteen, all di-tetrads.

4. There is a heterochromosome group of the 2 X type, consisting of twelve tetrad chromosomes in the early oocyte, and reducing to six di-tetrads before the first division.

5. Each of the chromosomes of the oogonia — diploid number — is potentially a dyad and becomes a tetrad by a longitudinal division during the early oocytic prophase I.

6. By a process of pseudo-reduction through parasyndesis these thirty-six tetrad chromosomes (diploid number) are reduced to eighteen di-tetrads (haploid number) in the late oocytic prophase I.

7. The first oocytic division is reductional, the second equational.

8. An egg (12 + 6) fertilized by a spermatozoon (12) forms a zygote (male) with thirty chromosomes (24 + 6).

An egg (12 + 6) fertilized by a spermatozoon (12 + 6) forms a zygote (female) with thirty-six chromosomes (24 + 12).

9. Both maturation divisions follow insemination.

10. The interkinetic period of both spermatocytes and oocytes is of considerable duration.

11. The cleavage centrosomes are entirely of male origin.

12. Diminution begins with the first division of each soma cell after being separated from the propagation cell.

13. The descendants of the sixth generation of the germ-track cell are purely propagational.

14. The Querkerbe, present in all cells of the germ-track, disappears in the chromosomes of the soma cells after diminution has occured. The Querkerbe is probably a sign of a plurivalent condition of a chromosome, never indicating the plane of a syndetic union or that of a maturation division.

Recent studies of the same and other material has brought out several additional features of importance. The spermatogonia show very definitely two greatly unequal karyosomes during their resting stages (fig. 34). The very early stages of Prophase I show the same two unequal karyosomes which later resolve themselves into chromosomes. The smaller chromatic body gives rise to six heterochromosomes and the larger to twelve autosomes (fig. 35). Each of these eighteen chromosomes develop a Querkerbe and, in addition, the six show a single longitudinal split while the twelve show a double cleft, thus furnishing Metaphase I with six tetrad and twelve di-tetrad chromosomes (fig. 36). Pseudo-reduction occurs early and a resting stage intervenes before the discrete prophase chromosomes appear in the haploid number. In the oogonia and early first oocytes, no such separate position of the heterochromosomes is found and all prophase chromosomes are resolved out of one large karyosome (fig. 37). These are in the haploid number (thirty-six) and become tetrads (fig. 38) before parasyndesis reduces them to eighteen di-tetrads. No resting stage occurs and the diploid number passes directly into the metaphase plate as di-tetrad chromosomes (fig. 39).

The fusion nucleus of the zygote shows either thirty or thirty-six dyad chromosomes (fig. 40-41). Diminution divisions occur in the soma cells of either the two-celled or the four-celled stages, apparently according to chance, as the cases are of about equal frequencies (WALTON, 1918, pl. 8-9). Comparison of the nuclei of soma and propagation cells show that the former (fig. 42-43) contains sixty to seventy-two monad chromosomes and the latter thirty or thirty-six dyads.

T. canis furnishes an example of an ascarid in which the haploid chromosomes are di-tetrads which reduce to dyads for the diploid form and to monads for the somatic chromosomes, doubling the number present by each reduction in complexity of structure. The diploid chromosomes are therefore equivalents of two somatic chromosomes, and in addition, a small amount of excess chromatin material which is extruded into the cytoplasm and lost at the time of the diminution divisions.

2. Heterakidae.

Heterakinae.

a) *Ganguleterakis spumosa* (Schneider) Lane. Small intestine of rats and others of the Rodentia.

Syn: *Ganguleterakis gangula* Lane.
Heterakis dahomensis Gendre,
Heterakis spumosa Schneider,

Several different species of the Heterakidae have been used as material for the study of gametogenesis by various investigators. Gulick (1911) made a study of *Heterakis dispar*, *H. inflexa*, and *H. vesicularis*, and with Boveri studied a Heterakis from the pheasant. The results of these two workers indicated a peculiar similarity of chromosome number and behavior in the Heterakis species studied. These four species are inhabitants of domestic fowls, three from chickens and geese, and one from domesticated pheasants. In all four cases the haploid number of chromosomes is five, and the diploid number is nine for the males and ten for the females. A single heterochromosome of the X type is present. The somatic cells do not undergo any diminution process and contain the same number of chromosomes as do the germ cells, i. e., nine or ten, depending upon the sex of the embryo. The haploid chromosomes are typically tetrads which reduce to monads in the spermatozoa and ova.

The present report is based upon the study of the gametogenesis of *Ganguleterakis spumosa* (Schneider) Lane from the rat, *Epimys norvegicus*.

The extreme tip of the testis is composed of a large coenocytic cell containing one large terminal and numerous smaller adjacent nuclei, all of which are undergoing active mitoses. These nuclei do not show a definite number of chromosomes at any time. The distal nuclei after their fourth division cut off a portion of the cytoplasm and become independent cells — the primordial germ cells. These are pushed down the tube for some distance by the formation of new cells behind them before further division occurs. Following a period of rapid multiplication, these spermatogonia enter a growth stage and metamorphose into p imary spermatocytes containing six centers of chromatin aggregation, four of which show a Querkerbe and two longitudinal splits (fig. 44); the other two show only one such cleft. The metaphase plates of the primary spermatocytes (fig. 45) show four di-tetrad and two tetrads. The latter fail to divide at the first division, and after some delay follow (fig. 46) the autosomes into one of the daughter plates. Two types of secondary spermatocytes are thus formed, one containing four and the other six tetrad chromosomes (fig. 47). The second division

separates the tetrads into dyads, giving rise to two types of spermatids, one of which contains four (fig. 48a) and the other six (fig. 48b) dyad chromosomes.

From the above, it seems that the haploid number of this Heterakid is six, four of which are autosomes and two, heterochromosomes. These two fail to divide in the first division, but do so in the second. They have the behavior of an X type, similar to that reported by Wilson (1909) for Syromastes, in which the X chromosome is bivalent, and one type of spermatozoon contains two more chromosomes than does the other. *G. spumosa* shows this same reaction, one-half of the spermatozoa having four and the other six chromosomes.

The early prophases of Oocyte I show twenty-four peripherally placed chromosomes, arranged in pairs and embedded in a linin network (fig. 49). These pairs unite and develop a Querkerbe (fig. 50), forming twelve tetrad chromosomes. Following a "bouquet" stage in which the chromosomes all clump up to one side of the nucleus, twelve chromosomes gradually reappear and after pseudo-reduction by parasyndesis, form six di-tetrad chromosomes, each with a Querkerbe and two longitudinal clefts (fig. 51).

The first division is along the plane of one of the longitudinal splits, and results in the formation of a secondary oocyte containing six chromosomes (fig. 52).

The second division is also along a longitudinal plane and results in a mature ovum with six dyad chromosomes (fig. 53).

The spermatozoon enters the egg between the first and second maturation divisions, and has established the male pronucleus by the time the second division is completed and the female pronucleus organized. The fusion nuclei show either ten (fig. 54), or twelve (fig. 55) dyad chromosomes, dependant upon the type of the contributing spermatozoon. The plasmosomes reappear after the fusion process is complete and continue until just before the metaphase plate of the first cleavage spindle is formed.

No process of diminution was observed, but while the embryonic germ cells retained either ten or twelve dyad chromosomes, the somatic cells after their first division all showed twenty-four monad chromosomes (fig. 56). As shown by the developing oogonial cells (fig. 49) which contained twenty-four chromosomal elements, the embryos which contain the twenty-four somatic chromosomes or the twelve dyad germinal elements, develop into adult females, and those containing twenty or ten, into adult male worms. The tendency to reduce to a monad condition in the germ cells as well as in the somatic cells is also shown by a study of the oogonia and early oocytes. In these cells the union of the chromosomes into dyads is so loose that they appear rather

as two chromosomes lying side by side as the members of a pair than as halves of a dyad body (fig. 49).

The study of spermatogenesis showed two chromosomes of the X type. Under such circumstances, the expected number in the female would be the 2 X condition, or four chromosomes. The male showed eight autosomes and two idiochromosomes for the diploid number. The female showed twelve chromosomes, of which eight are autosomes and four the heterochromosomes, thus fullfilling the expected conditions. In the haploid state, the male shows four di-tetrad autosomes and two tetrad idiochromosomes; six in all. The female shows six di-tetrad chromosomes, two of which represent the 2 X condition of the X chromosomes in the male, i. e., two di-tetrads as the 2 X stage of two X tetrads such as are found in the male.

Ganguleterakis spumosa furnishes an example of compound chromosomes, the simplest form being found in the somatic cells. These are united more or less closely into pairs in the germ cells, becoming definite dyads in the early spermatocytes and oocytes. By parasyndesis and an additional longitudinal split the autosomes and the female heterochromosomes become di-tetrads while the male heterochromosome only becomes a tetrad (has no synaptic mate). By the two maturation divisions the di-tetrads and tetrads are reduced to the dyad condition in the fusion nucleus. The diploid chromosomes are di-tetrad, reduce to dyads through two divisions for the haploid condition, and finally to monads in the somatic cells. There is no evidence of a separate karyosome for the heterochromosomes during the resting periods of any stage. The fact that the structural composition, as well as the numbers, of the chromosomes differs so much from that of the other Heterakidae studied heretofore, justifies — on cytological grounds — the removal of this form from the genus *Heterakis* to the genus *Ganguleterakis*, of which the type species — *G. gangula* — has been regarded as being identical with *Heterakis spumosa*. In both cytology and morphology *Ganguleterakis* is intermediate between the *Ascaridae* and the *Heterakidae*. It may well be that a cytological analysis is advisable in determining the final systematic position of debatable forms, especially among those genera in which the cytological content is known to be peculiarly uniform.

b) *Heterakis papillosa* (Bloch) Railliet. From the caecum of *Gallus domesticus* (the domestic fowl).

Syn: *Ascaris galli* Schrank,
Ascaris gallinae Gmelin,
Ascaris gallinarum Schrank,
Ascaris inflexa (Zed.) Rudolphi (in part),

Ascaris papillosa Bloch,
Ascaris teres galli minor Rudolphi,
Ascaris terer (*minor*) Dujardin,
Ascaris teres (*minor, phasiani-galli et pictu*) Rudolphi,
Ascaris tetraonis Gmelin,
Ascaris undulosa-striata Baird,
Ascaris urogalli Rudolphi,
Ascaris vesicularis Froelich,
Fusaria papillosa (Bloch) Zeder,
Fusaria reflexa Zeder (in part),
Fusaria tetraonis (Gmel.) Zeder,
Heterakis vesicularis (Froel.) Dujardin.

The material for this study was obtained from the caeca of domestic fowls killed at Champaign, Illinois, during February and March.

Since *H. papillosa* has been regarded by some authors as a synonym for *H. vesicularis*, the present writer decided to make a careful study of gametogenesis of material identified as *H. papillosa* in order to make comparisons with the accounts of Boveri and Gulick for *H. vesicularis*. The results agree in many respects but diverge in several important points, so much so that the synonomy of the two names is probably only partially true, *H. vesicularis* being the broader term.

The spermatogonia show definitely eighteen small monad chromosomes (fig. 56) instead of the nine reported by Boveri and Gulick. During the growth period of the primary spermatocytes, sixteen of these monads undergo two pairings and a longitudinal split, resulting in four di-tetrad chromosomes; the other two monads pair and form a tetrad by means of the longitudinal cleft (fig. 57). This tetrad is the heterochromosome. Gulick describes parasyndesis of dyads to form tetrads, the heterochromosome remaining as a dyad.

The metaphase plate (fig. 58) contains fourdi-tetrads and one tetrad, the latter failing to divide at the first division and lagging behind the autosomes in their progress to one of the two poles of the spindle. Two types of secondary spermatocytes result from this division, one having four and the other five tetrad chromosomes (fig. 59a and b). According to Gulick these chromosomes were dyads, not tetrads.

The second division is equational, resulting in two types of spermatids; one containing four, and the other, five dyads (fig. 60a and b).

The resultant spermatozoa (fig. 61) show a clumped, saucer-shaped chromatic mass. No evidences of a "residual body" were found. Gulick and Boveri both failed to observe any such bodies in their material.

Gulick reported that not only the spermatogonia, but also the oogonia show a definitely separate karyosome out of which the heterochromosomes are resolved. The present study fails to show this phenom-

enon in either sex of the primordial germ cells. A separate karyosome was formed by the idiochromosome at the time of syndesis in the male, eight of the chromosomes forming a common mass of chromatic material and the heterochromosome remaining separated. No evidence of any such isolation of idiochromatic material was found at any stage of oogenesis.

The early prophase nucleus of the primary oocyte shows the presence of ten tetrad chromosomes, all of which undergo pseudo-reduction to five di-tetrads (fig. 62) before the first maturation division occurs. These five di-tetrad chromosomes reduce to five tetrads at the first division and to five dyads at the second (fig. 63). The female pronuclei all contain five dyad chromosomes and the two types of male pronuclei contain four and five dyads, respectively.

The eggs are deposited by the female before the two pronuclei are completely fused, and therefore no material showing the fusion nucleus or early cleavage phenomena was obtained. The presence of a diminution division was not determined. The question of reduction of the dyad chromosomes of the diploid number to a monad condition in both the germ cells and the soma cells could not be answered by direct observation on embryonic material, but evidences gained by study of the adult material point to the probable explanation. The spermatogonial cells (fig. 56) showed eighteen monad chromosomes and point to a probability that the embryonic germ cells assumed a tetraploid condition sometime during their development, perhaps after their isolation from somatic relationships. Intestinal cells from the adult worms also show the tetraploid number of monad chromosomes, in the case of the male these were eighteen in number (fig. 64). Other somatic nuclei showed to a lesser degree the doubling of the diploid chromosomes and the reduction of the dyad condition to that of a monad.

As the pronuclei approach each other preparatory to fusing, a heavily staining body appears in the cytoplasm and assumes a position near the more centrally located centrosome of the newly forming cleavage spindle. This body is quite regular in outline, usually appearing as a four-parted structure. It stains as does cytoplasm when differential stains are employed. It does not have any relation to the newly forming cleavage spindle except the accidental one of location. Its origin is doubtful, as no traces of its appearance were observed until just before the two pronuclei began their migration toward each other. Its fate is also as yet unknown, since no material showing the fertilized egg and early cleavage is available for studies of its behavior. Because of the cytoplasmic nature of its staining reactions it eliminates the possibility of it being a "chromatoid body", a "paranucleus", or a "Nebenkern". If of nuclear origin at all, it could only be of achromatic material,

and no evidence of any such extrusion has been observed. The possibility of it being a "yolk nucleus" is probably obviated by the fact that such bodies are not reported from Nematodes, and in the animals where they do appear, the "yolk nuclei" cease to function and disintegrate before the first maturation division. In *H. papillosa* this body has no forerunner in the growth or maturation stages that could be recognized as such. The possibility of its entrance with the spermatozoon is not probable. The male pronucleus includes all of the nuclear material of the spermatozoon, the new cleavage centrosome figure is formed from that of the male, and no "residual body" is present that might transform into this new body. Careful staining failed to show any relationship between this body and a Golgi apparatus or a mitochondrial mass. The interpretation which seems the most logical is that this body is the visible sign of the metabolic changes which accompany the breaking down of the egg centrosome and its archoplasmic sphere. The position of this body is identical with that of the egg centrosome, and it does not appear until after that body has ceased to function and has apparantly disappeared at the approach of the cleavage astrosphere of male origin. If this body is the degenerating female astrosphere, the non-chromatic nature of its staining reactions are explained, its sudden appearance as the two pronuclei approach and its gradual diminution as they fuse are understandable, and its location is favorable. That this body is not an artifact due to fixation is shown by its appearance after fixation by formol, acetic alcohol, glycerine alcohol, PETRUNKEVITCH, BOUIN and CARNOY-Phenol. The body appeared in every egg showing the two pronuclei, and in every one of the twenty-eight worms examined.

Study of gametogenesis of *H. papillosa* shows the diploid number to be nine and ten, the haploid, four and five in the male and five in the female, and the tetraploid number in the somatic and primordial germ cells to be eighteen and twenty. The diploid chromosomes are compound structures, equivalent to two simple somatic chromosomes.

B. Filaroidea.

1. Acuariidae.

Acuariinae.

a) *Acuaria* (*Dispharynx*) *spiralis* (Mol.) Railliet, Henry et Sisoff. From the proventriculus of *Quiscalus quiscala* (Bronzed Grackle).

Syn: *Acuaria laticeps* (Rud.) R. H. & S.,
Dispharagus involutus (Linst.) Stossich,
Dispharagus laticeps (Rud.) Dujardin,
Dispharagus spiralis Molin,

Dispharynx spiralis (Mol.) Skrjabin,
Filaria involuta Linstow,
Spiroptera fallax Siebold,
Spiroptera laticeps Rudolphi.

The material for this study was obtained from Grackles collected at Urbana Illinois during their fall migration.

Study of gametogenesis showed that the germinal elements are very small and that the chromatic material tends to clump up to such a degree that the most careful searching was necessary to find nuclei that were well enough preserved to permit the counting of the chromosomes. The following account is therefore only tentative, in that the evidence at hand seems to indicate the conclusions reached, but a far larger amount of favorable material is necessary in order to perfectly complete the study.

The few spermatogonial nuclei observed showed anywhere from nine to fourteen chromatin bodies, some of larger size than the others. Usually there was a mass of clumped material in addition to the isolated bodies. The average number seemed to be twelve. These bodies were quite irregular in outline, so much so that no evidences of any Querkerbe could be found. Whether they are monad or dyad in structure therefore remains unsettled. In the resting nuclei there consistantly appeared two very unequal chromatic bodies as well as a distinct plasmosome.

During the entire course of the "growth" zone a definitely staining chromatic element remains isolated and does not enter into any stage that permits synezesis to occur. This body probably represents the heterochromosome. The late prophase shows approximately eleven small chromosomes that have no indications of the Querkerbe or of any longitudinal constriction. A second "diffuse" stage follows, the heterochromosome again failing to take part. Resulting from this last period of disappearance of the chromosomes, six new chromatic bodies arise and enter the metaphase of the first spermatocytic division. No details of their structure were clearly enough shown to be accurately determined. In all probability they are at least tetrads in structure as are those of all other of the Nematodes studied.

The first division shows one very definitely lagging chromosome which is probably the heterochromosome since it fails to divide at this time. By its failure to divide, half of the secondary spermatocytes receive one more chromosome than does the other. Definite counts of chromosomes were very few and all showed six present. The clumping of the chromosomes was so consistant that no cases of the expected five chromosomes were found. Measurements of the clumped mass were not successful in showing two types according to volume as the amount of clumping varied greatly from cell to cell.

The second division showed no lagging or failure to divide on the part of any of the chromosomes. Careful examination of the anaphase plates of this division was made in the hope of ascertaining the presence of dyad or monad conditions of the resultant chromosomes, but the few cases found universally failed to show the structure of the chromosomes. They appear as small round or ovoid bodies, often irregular in outline.

The spermatides are at first filled with very heavily staining deutoplasm, but as metamorphosis proceeds a small amount of this material gathers at one end of the cell to form the "Glanzkörperchen" of the mature spermatozoon and the rest is cast out of the cell by a cytoplasmic division of the nature of a "cytophore" formation process. These cytophore bodies quickly degenerate, leaving enormous numbers of mature spermatozoa in the seminal vesicle. This structure is very large in comparison with the usual ratio of seminal vesicle to the entire testis length. The female shows very few spermatozoa in the seminal receptacle. These two facts, togather with the absence of a large nutritive mass in the spermatozoon, argue strongly for the fact that copulation occurs only at infrequent intervals and that both males and females accumulate large numbers of matured germ cells between these times. Copulation, when it occurs, is followed by only a very short period before the eggs are all fertilized. The unused spermatozoa degenerate immediately because of their lack of nutritive material in storage, and hence a large receptaculum is not needed to store them up for slow delivery to the gradually maturing eggs as these become ready for insemination. The female carries the eggs until the larvae are practically ready for hatching and then deposits them in a short period of time. This is inferred from the fact that the larvae are approximately all of the same age. Meanwhile both sexes are storing up another mass of maturing spermatozoa and unfertilized eggs. The more or less permanent attachment of the worms to the mucosa strengthens this supposition. Each worm lies with its head embedded in the mucosa and in all cases examined by the writer, they were at such intervals from each other that the possibility of copulation without one or the other becoming free was almost negligible, especially as the spicules of the male are quite short and the vulva of the female is anterior to the mid-region of the body. That the males are most probably the ones which move is shown by the fact that of the seventy-six males collected from eight different hosts, ten were found free in the lumen of the proventriculus. Of the one hundred and twenty females collected from the same hosts, none were found detached.

Study of oogenesis was fully as unsatisfactory as was that of spermatogenesis. Chromosome numbers in the oogonia ran as high as twenty-

one. The average number appeared to be about twelve. From these numbers it seems possible that the germ cell chromosomesare usually dyad in structure, with a tendency to reduce to a monad condition in the primordial germ cells. Study of somatic cells did not throw any further light on this question of chromosome structure. A second period of diffused chromatic material was followed by the appearance of six discrete chromosomes, each of which showed a single longitudinal split which disappeared before mitosis began.

The first division shows no lagging, each daughter cell receiving six chromosomes, the structure of which could not be determined. At this period the nucleus enters a long resting stage and continues in this condition until insemination occurs. The nucleus has again resumed a central position in the egg. After the entrance of the spermatozoon, the oocyte nucleus again becomes active and migrates to the periphery of the cell at a point opposite the place of entrance of the spermatozoon and sets up the second maturation spindle. The resulting egg nucleus contains six small rod-shaped chromosomes. The two pronuclei are formed and approach each other, the chromosomes meanwhile losing their distinct outlines and becoming reticular. After the fusion of the pronuclei, the chromosomes again reappear as discrete bodies and form the first cleavage spindle. The expected numbers of eleven and twelve were not observed, as in no case were more than eight separate chromosomes found. A clumped mass of the chromatic material always accompanied the distinct chromosomes, varying inversely in size with the number of recognizable chromosomes.

Careful examination of the numerous embryos showed that there actually are the two types of zygotes formed, as a few propagation cell nuclei were observed to contain eleven chromosomes in some cases and twelve in others. No evidences of a diminution division were found during the examination of a large number of somatic cell mitoses.

As mentioned above, there is some proof that the germ cell chromosomes are dyad in structure since the oogonia in some cases tend to show more than the expected diploid number of twelve. None of the embryonic somatic cells showed clear enough pictures of mitotic figures to permit a determination as to whether a similar tendency was present in them as well as in the oogonial cells. A simple monad condition should show here, if anywhere. Nuclei from the somatic cells of the adult worms, especially from the intestinal wall, showed that the expectation is entirely justifiable as counts of as high as twenty-one were obtained. A perfect example should have shown twenty-four monad chromosomes.

Study of the gametogenesis of *Acuaria spiralis* has shown that the diploid numbers are most probably eleven and twelve for the male and female individuals and the haploid numbers are five and six for the

males and six for the females. The heterochromosome is of the X type. It seems probable that the diploid chromosomes are dyad in structure, with the union of the two monad halves so well established that their separation is the exception, not the rule. The heterochromosome apparently is separated from the autosomes in the primordial germ cells and retains its identity throughout the whole life cycle by forming a separate karyosome during every interkinetic period.

Physalopterinae.

a) *Physaloptera turgida* Rudolphi. From the stomach of the Opossum (*Didelphys virginiana*).

Syn: *Spiroptera didelphidis-virginianae* Leidy,
Spiroptera turgida (Rud.) Dujardin,
Turgida turgida (Rud.) Travassos.

The spermatogonial nuclei contain two unequal karyosomes and one or more small plasmosomes during their long resting period. During their division stages the chromatin of these cells is so clumped that accurate counts of chromosome numbers was impossible.

The growth period of the primary spermatocytes is of rather short duration, the spermatogonia having been slowly growing insize as they multiplied in numbers. During this period the chromatin is rather diffusely scattered throughout the nucleus, showing consistantly, however, ten more or less irregularly shaped centers of chromatin aggregation.

At the end of the growth period these centers come to lie side by side in pairs and as the definite chromosomes are formed as a result of the condensation of the different chromatic materials, it is evident that pseudo-reduction has occured. The five resultant chromosomes show a definite longitudinal cleft as well as the Querkerbe. The chromosomes arrange themselves in the metaphase plate (fig. 65) so that the plane of the first division is longitudinal, but not along the plane of parasyndesis. The first division shows four of the chromosomes dividing, and one failing to do so, although it lags behind and becomes considerably elongated. Both early and late anaphases show that the lagging chromosome fails to divide, but eventually passes to one of the poles of the maturation spindle. During the entire progress towards the pole, the heterochromosome is accompanied by another chromosome. From examination of this stage it seemed that there must be two members to the sex chromosome group (fig. 66), but careful study of earlier stages and also of the second spermatocytes show that there is actually only one idiochromosome. This is apparently very closely connected to one of the autosomes, and due to this connection, that chromosome is retarded greatly in its migration to the pole of the

spindle. This behavior is quite similar to that reported for the heterochromosomes of *Contracaecum incurvum* (*Ascaris incurva* — GOODRICH, 1916). The definite linin fibers visible in that species were not apparent in *Physaloptera turgida*.

The metaphase plates of the two types of second spermatocytes show four and five chromosomes as a result of the reductional first division (fig. 67a, 67b). These chromosomes are potentially tetrads since in the following division they separate along a plane passing through the long axis of each chromosome, and not in the plane indicated by the Querkerbe. There is no visible indication of this second plane of division so that the chromosomes appear to be dyads.

In the second division there is no indication of lagging on the part of any of the chromosomes, all of which have undergone a equational division. Figures of the anaphase plates (fig. 68a, 68b) show that each of the spermatids is to receive either four or five dyad chromosomes. The one type of spermatid, and the resultant spermatozoon as well, receives four dyad autosomes, and the other, four dyad autosomes and one dyad heterochromosome. The sex chromosome in the males of *Physaloptera turgida* is of the X type, with X equaling one.

The oogonia undergo a series of very rapid divisions during their multiplication period, showing in every case ten small dyad chromosomes. During the early growth period the young oocytes show ten small rod-like chromosomes, often arranged side by side in pairs. As the cells mature these pairs of chromatin rods fuse and develop into five discrete chromosomes (fig. 69). Two of these are formed before the others. From a comparison with conditions as found in *Rhabdonema nigrovenosa* (SCHLEIP, 1911), one of these is probably the sex chromosome that differentiates earlier than the autosomes. The other chromosome probably corresponds to that autosome found in the male which is apparently so closely linked to the idiochromosome. The early prophase chromosomes show a distinct Querkerbe and shortly before their arrangement in the metaphase plate (fig. 70) they show a definite longitudinal split. The first division is along the plane thus indicated.

The four autosomes divide before the heterochromosome and its accompanying autosome show any evidences of activity. The autosome then slowly divides and after still further delay one-half of it, together with one-half of the now divided idiochromosome, migrates to each of the two resultant sister plates of this division (fig. 71). Such a lagging of the heterochromosome during division is unusual in the oocytic meiosis, but seems to occur with great regularity in the material studied. These two chromosomes are somewhat larger than the four autosomes and the greater length of time required for division may simply be due to their greater mass, and not to the fact that one is an idiochromosome

and the other closely associated with it. Such an interpretation would be more in line with the ordinary course pursued by oocytic chromosomes in general.

Metaphase plates of the second oocytes (fig. 72) show that there are five dyad chromosomes present, two of which are slightly larger than the other three. The first polar cell also shows five chromosomes. A second longitudinal split has appeared and forms the plane along which the second division proceeds.

The second division shows no lagging of any of the chromosomes and telophase plates (fig. 73) show that five dyad chromosomes remain in the egg and five have entered the second polar cell. Two of these chromosomes are slightly larger than the others.

The spermatozoon enters the egg before the first maturation spindle migrates to the periphery of the cell and remains in a resting condition until the first division is completed. The spermatozoon nucleus then migrates toward the middle of the cell and organizes a typical pronucleus during the anaphase of the second oocytic division (fig. 73). After the second division is completed the female pronucleus is organized with five dyad chromosomes present. The pronuclei then migrate toward the center of the cell and form the fusion or cleavage nucleus. The two types of spermatozoon pronuclei — one with four and the other with five dyad chromosomes — can be distinquished (fig. 74, 75). Often one or both pronuclei may contain a transient plasmosome.

The metaphase plates of the fusion nucleus show either nine (fig. 76) or ten (fig. 77) dyad chromosomes. In the first case there are three chromosomes definitely larger than the others — two autosomes and one heterochromosome —, and in the other four large dyads — two autosomes and two heterochromosomes. The early anaphase shows that each dyad has undergone a longitudinal division and still retains the Querkerbe.

The second division of both cells is by ordinary mitosis, with no signs of any diminution, nor does it appear at any later stage. Fig. 78 is of a female-producing embryo having ten dyad chromosomes, only two of which — the heterochromosomes — are larger than the others. Fig. 79 shows the metaphase plates of a male-producing embryo which contains only the one large idiochromosome in each cell. Only a few embryos were found in which the soma cells contained double the number of chromosomes that are present in the germ track cell (fig. 80). In the embryo figured the germ cell contains nine dyad chromosomes while the soma cell shows eighteen monads, with no apparent size dimorphism detectable.

Physaloptera turgida has a diploid number of ten dyad chromosomes in the female and nine in the male. Of these chromosomes, one auto-

some and the idiochromosome are somewhat larger than the other autosomes. The haploid number for the female is five tetrad chromosomes which undergo two longitudinal splittings and reduce to dyads, thus making the haploid bodies essentially di-tetrads, although the second longitudinal split does not occur until after the first division is completed. The haploid number for the male is also five, four of which are di-tetrad in potential and one tetrad, although all fail to show the plane of the second division until in prophase II.

The lagging of the one autosome that is in such close relation to the idiochromosome is very characteristic, and also quite unusual since no visible bonds of connection between the two chromosomes were demonstrated. This relationship is the more peculiar in that it exists in both the spermatocytes and the oocytes. A somewhat similar case was reported by Goodrich (1916) for *Ascaris incurva* (*Contracaecum incurvum*), but there the connections were demonstrable in the spermatocytes only. No relation, actual or apparent, existed between the autosomes and the idiochromosomes in the oocytes.

Physaloptera turgida does not show any signs of a diminution division, but in isolated instances the soma cells show double the number of chromosomes of half the size of those present in the germ cells. This shows that the germ cells are actually compound as to the structure of their chromosomes, reducing through the two maturation divisions from a di-tetrad condition to ultimate monad, i. e., the simplest state, in the somatic cells of the embryo.

2. Spiruridae.

Spirurinae.

a) *Protospirura muris* (Gmel.) Seurat. From the stomach of *Microtus pennsylvanicus.*

Syn: *Ascaris muris* Gmelin,
Ascaris obtusa Froelich,
Filaria muris (Gmel.) Stossich,
Filaria obtusa (Froelich) Schneider,
Fusaria muris (Gmel.) Zeder,
Lumbricus muris (Gmel.) Rudolphi,
Lumbricus muris domesticae minoris Werner,
Spiroptera brauni von Linstow,
Spiroptera obtusa (Froel.) Rudolphi.

Study of the spermatogonia of *P. muris* did not show any cells in which a definite or even an approximate count of the chromosomes could be made. The material was well preserved, but mitotic figures were exceptionally rare and in no case was a face view of a metaphase plate obtained. The chromosomes were too small to enable the observer

to decide whether they were monad or dyad in structure; at least a definite Querkerbe could not be distinguished, although study of the cells from the embryo led to the belief that such a condition should exist, as the chromosomes are dyad in nature when they retain the same construction and number as the cells of the embryonic germ track. Careful observation of resting nuclei failed to show any consistant number of karyosomes or plasmosomes, the former varying from one to five in different cells within the same animal. Such chromosomes as could be found were all practically of a uniform size.

The early spermatocytes, after about the middle of the growth period, showed nine very distinctly dyad-like chromosomes, all of about the same size, and with the Querkerbe distinctly developed. Shortly before the end of the growing period, these chromosomes become diffused throughout the nucleus and when they reappear, they are in the form of five larger bodies, each showing a distinct transverse constriction and a faint longitudinal cleft. In addition, four of them also show a second longitudinal cleft at right angles to the plane of the first.

The metaphase plate (fig. 81) contains four di-tetrad and one tetrad chromosomes. The first division is along the plane of parasyndesis, the di-tetrads separating into tetrads and the original tetrad failing to divide. This chromosome is the heterochromosome and is of the X type, hence its failure to divide makes the first division reductional for all of the chromosomes. The X body lags considerably at the time of the division of the autosomes, but eventually passes to one pole. As a result of this division two types of daughter plates are formed, one with four tetrad autosomes and the other with the four tetrad autosomes and the tetrad idiochromosome (fig. 82, 83).

The second division is equational, each chromosome separating along the plane of its longitudinal cleft. The resultant spermatocytes are of the two types, the one with four dyad autosomes (fig. 84) and the other with the four autosomes plus the dyad heterochromosome (fig. 85). Two types of spermatozoa resulted by metamorphosis, but no measurements were made to determine any size dimorphism of the nuclear contents.

The description applied to the spermatogonia applies to the oogonia as accurately. Nothing definite concerning the number or structure of the oogonial chromosomes could be determined.

As in the spermatocytes, the first appearance of the distinct countable chromosomes was during the early first prophase of the oocytes, and showed them to be all dyads in structure. The number was ten, as would be expected from the fact that in the male the number was nine and an idiochromosome of the X type was present. The reduced number of chromosomes is five, each of which possesses a Querkerbe and two longitudinal indications of future planes of division.

The first division separates the five di-tetrad chromosomes (fig. 86) along one of the indicated longitudinal planes, furnishing the secondary oocyte with five tetrad bodies (fig. 87). The second division further reduces these, again by longitudinal fission, to five dyads (fig. 88). The mature ovum contains five dyad chromosomes.

Examination of the pronuclei shows that the female nucleus possesses in all cases the five dyad elements and that in half of the cases the male nucleus contains four chromosomes and in the other half, five. The fusion nuclei of the zygote also shows the sexual dimorphism in chromosome numbers, the male-producing cell containing nine dyad elements (fig. 89) and the female-producing cell, ten (fig. 90).

As far as could be determined, no process analogous to a diminution reduction of the somatic chromatin occurs. The chromosomes of the soma cells also fail to undergo any further splitting in spite of their dyad condition; retaining the characteristic diploid number for the sex.

Protospirura muris is closely alled to the Ascarids from a morphological point of view, but shows less affinities from the cytological stand-point. While it possesses the di-tetrad chromosomes similar to those of many of the Ascaridae, it fails to show any diminution of chromatin and no increase in number of chromosomes in the soma cells over those of the germ-track cells. It perhaps illustrates a condition in which the union of chromosome elements is so firm that separation in the soma cells is no longer usual or even occasional, although the mark of the point of union — the Querkerbe — is still visible. This double nature of the diploid chromosomes persists through pseudo-reduction so that the haploid chromosomes are di-tetrad even though the Querkerbe ceases to mark the plane of a final division of the chromosomes into their morphological units. The next step in such a series would be a condition in which the Querkerbe is present only in the somatic cells and never in the germ cells and finally, all trace of any such constriction should disappear completely and the chromosomes of the germ cells appear as tetrads and the soma cell chromosomes as monads. This final condition is found in such forms as *Belascaris mystax*.

C. Oxyuroidea.

1. Cruzidae.

Cruziinae sub-fam. nov.

a) *Cruzia tentaculata* (Rud.) Travassos. From the stomach and small intestines of *Didelphys virginiana*.

Syn: *Ascaris tentaculata* Rudolphi,
Oxysoma tentaculatum (Rud.) Schneider,
Oxysomatium tentaculatum (Rud.) Railliet et Henry.

Study of the spermatogonia show that typically twelve small dyad chromosomes are present in each nucleus. Occasionally a nucleus showed more than twelve chromosomes. In such cases careful examination determined that several were monad in structure, and if the monads were paired up, the total of pairs never exceeded twelve.

During the growth period, the chromosomes lose their stainability and become diffused throughout the linin ground-substance of the nucleus. Toward the end of this period a single dyad-like chromosome appears somewhat before any of the others (fig. 91). This chromosome usually is made up of two elements which represents two of the spermatogonial dyads inasmuch as only ten other chromosomes (fig. 92) reappear after the diffuse stage. These twelve chromosomes undergo a syndesis stage and reappear in the form of six large chromosomes, each showing a Querkerbe. Two longitudinal clefts appear in five of the chromosomes, thus making them di-tetrad in structure. The sixth shows only one such split, and hence is only a tetrad.

Study of the metaphase plates (fig. 93) show that one of these chromosomes is almost one-fourth larger than the others, and that this is the tetrad noted in the prophase. During the anaphase this large chromosome fails to divide and lags considerably in its passage to one of the daughter plates (fig. 94). The division is thus reductional, at least as far as the heterochromosome is concerned. This body is clearly of the X type, with X equaling one.

Two types of secondary spermatocytes are formed by this division, one possessing five autosomes and the other five autosomes plus the large idiochromosome. Study of the metaphase plates (fig. 95, 96) show that all of the chromosomes are tetrads. The anaphase of the second division shows that every chromosome has undergone a longitudinal splitting, and that none of the chromosomes lag at all in their progress toward the poles.

Two types of spermatids are formed, one with five (fig. 97) and the other with six dyad chromosomes (fig. 98). These metamorphose into two types of spermatozoa. No size dimorphism of the nuclei of the spermatozoa was observed, although theoretically a bimodal curve should be obtained by plotting the volume measurements of a large number of nuclei.

Cruzia tentaculata shows a diploid number of twelve dyad chromosomes which reduce through parasyndesis to five di-tetrads, and in the case of one-half of the cells, to six. The sixth chromosome is a tetrad idiochromosome of the X type. The mature spermatozoa also contain five and six chromosomes, all of which are dyad in structure.

The oogonia of this species are very small and the chromatic material is so clumped that accurate counts were impossible. Such few counts

as were obtained varied greatly, metaphase plates showing anywhere from ten to twenty-one small rod-shaped chromosomes.

In the early prophase of the primary oocytes, the chromosomes appear very distinctly as small rod-shaped bodies, usually arranged in pairs. Counts of a large number of nuclei showed that twelve such loosely coupled pairs were present; in many cases the individual members of a pair were not as yet united and counts of the componant elements were necessary to determine the number of chromosomes as twenty-four in every case. These separate rods of chromatin after this side-by-side pairing formed twelve discrete chromosomes, each of which showed a definite cross constriction or Querkerbe.

Pseudo-reduction, probably by parasyndesis, occurs during the late prophase, and results in the formation of six chromosomes, all of which show the Querkerbe and two definite longitudinal clefts. One of these chromosomes is distinctly larger than any of the others. By analogy with the conditions in the male, this large chromosome represents the 2 X phase of the heterochromosome in the female.

The metaphase plates of the first division show six chromosomes (fig. 99) arranged so that the plane of cleavage passes through one of the longitudinal splits formed during the prophase. This division is reductional in that each chromosome is halved along the plane of parasyndesis so that each daughter anaphase group receives six tetrad chromosomes, one of which is larger than the other five.

The second division is equational in the sense that the plane of separation passes through the remaining longitudinal cleft. These tetrad chromosomes (fig. 100) are divided into dyads, the ovum retaining six and the other six being lost in the second polar cell.

The female pronucleus when organized after the division is complete, contains six dyad chromosomes (fig. 101), one of which is larger than the others. The male pronucleus contains either six dyad chromosomes — five autosomes and one heterochromosomes (fig. 102) — or five dyad autosomes (fig. 103). The fertilization nuclei are of two types, one containing twelve dyad chromosomes, two of which are large heterochromosomes, and one containing eleven dyads, only one of which is the heterochromosome.

The eggs are laid in the one-celled stage and as no embryos were found, it was impossible to determine the presence or absence of a diminution reaction, or whether the dyad chromosomes of the germ track cells reduced to double the number of monad bodies in the soma cells.

Study of oogenesis has shown that the diploid number of chromosomes is twelve and the haploid number six. One of these six chromo-

somes represents the X chromosome of the egg in accordance with the expectation resulting from the study of spermatogenesis. This chromosome is the largest of the group. There is no evidence of the separate position of the heterochromosomes during oogonial or oocytic resting stages. *Cruzia tentaculata* does show evidence of the compound nature of the germinal chromosomes in that there are present di-tetrad forms which are reduced by the two maturation divisions to dyads. Although no direct observations as to the reduction to the ultimate monad condition were available, yet such a condition is highly probable from the observation that the chromosomes of the early Prophase I appeared as small rod-like monad bodies, tetraploid in number. and undergoing parasyndesis to reduce to the diploid number of dyad-like late prophase chromosomes.

2. Oxyuridae.

Syphaciinae.

a) *Syphacia obvelata* (Rud.) Seurat. From the caecum of *Epimys norvegicus.*

Syn: *Ascaris dipodis* Rudolphi,
Ascaris obvelata Rudolphi,
Ascaris oxyura Nitzsch,
Ascaris tetraptera Nitzsch (in part),
Ascaris vermicularis muris Froelich,
Fusaria obvelata (Rud.) Zeder,
Oxyuris obvelata (Rud.) Dujardin,
Oxyuris stroma Linstow (in part).

A considerable amount of material of this worm was obtained by examination of fecal matter and by dissection. Careful study of smear mounts and of sections was made, but the germ cells were so minute that but little could be made out concerning gametogenesis. The male is heterozygous for sex and the female homozygous, the mature spermatozoa containing seven and eight chromosomes and the ova eight. The reduction division in the male is the first; two types of second spermatocytes being formed. There is a definitely lagging chromosome present in this division. The diploid numbers were found to be fifteen and sixteen. No diminution divisions were observed, and the soma cells showed practically the same number of chromosomes as did the germ cells, at least as far as their small size enabled accurate counts to be made. Presumably the diploid chromosomes are monads and the haploid, tetrads, since there is no evidence of a Querkerbe and difference in number between those of the germ and of the soma cells.

D. Strongyloidea.

1. Trichostrongylidae.

Heligmosominae.

a) *Nematospira turgida* Walton. From the stomach and duodenum of *Microtus pennsylvanicus* (see Walton 1923, p. 61.)

Study of the spermatogonia shows the presence of small dyad chromosomes in all of the actively dividing cells from the blind end of the testis down through the zone of multiplication. Favorable nuclei were difficult to find, but such as were observed showed definitely eleven dyad chromosomes. Body cells were not found that gave a definite picture of division, but in all cases observed the number ran considerably above eleven, and the chromosomes did not show any signs of a transverse constriction, being evidently monad in character.

During the growth period the chromosomes lose their stainability and become diffused throughout the nucleus with the exception of one dyad (fig. 104). This body never entirely loses its distinctly solid form and hence can not enter into any syndetic relations with other chromosomes. The other ten chromosomes which disappeared at the beginning of the diffuse stage undergo syndesis and reappear as five large dyad chromosomes which immediately show two longitudinal clefts. Inasmuch as the cross-constriction does not indicate the future plane of either division, it must represent the original Querkerbe of the spermatogonial chromosomes and the syndesis was "side-by-side", parasyndesis. The chromosomes which failed to undergo syndesis shows one longitudinal cleft, thus being tetrad in structure while the others are di-tetrads. This chromosome is the heterochromosome. The metaphase plates show this chromosome either as the center member, or more commonly as the eccentrically placed member (fig. 105).

The idiochromosome lags definitely during the first division, failing to divide. As a result the two daughter nuclei receive four and five chromosomes (fig. 106, 107), now all tetrads. The second division separates all of the chromosomes along a longitudinal plane and results in the formation of two types of spermatids, one with five dyad autosomes and the other with the five autosomes and one dyad idiochromosomes six in all.

The spermatozoa developing from these spermatids show no distinguishable size dimorphism of the nuclei. A typical "Glanzkörper" is present which undergoes absorption from the center outwards as the spermatozoa ascend the uterus and are stored in the seminal receptacle (fig 108).

Study of the oogonia shows that twelve dumb-bell shaped chromosomes are formed at each multiplication mitosis and are completely

lost to view in each "interphase". At the beginning of the growth period after the last oogonial division has been completed, the chromosomes become diffuse and disappear entirely. That chromatic material wich retains any affinity for stains is found in the form of karyomeres located at the nodes of the linin reticulum. In the late prophase of the first division, the chromatic material again collects into discrete chromosomes, each of which shows the Querkerbe, and in addition, a single longitudinal cleft. The twelve dyads are reduced to six tetrads by the pairing of homologous chromosomes during this state of invisibility. A second longitudinal cleft at right angles to the first soon appears, making each chromosome di-tetrad in composition.

The metaphase plates of the primary oocytes (fig. 109) thus contains six di-tetrad chromosomes. The first division passes through the longitudinal cleft representing the plane of parasyndesis, and therefore is reductional in nature. Each secondary spermatocyte receives six tetrad chromosomes (fig. 110). These undergo the second longitudinal division which is now equational and results in the formation of ova, each possessing six dyad chromosomes.

Insemination occurs about the time of the throwing off of the first polar cell, the egg, now free from the rhachis, entering the receptaculum and becoming surrounded by the amoeboid spermatozoa during Metaphase I. A single spermatozoon enters and the fertilization membrane is completed as the polar cell is formed. The spermatozoon nucleus is usually not compacted into a solidly staining body as is commonly the case with Nematode spermatozoa, but with the exception of the short period before reaching the receptaculum of the female, each nucleus shows definitely its five or six dyad chromosomes. These arrange themselves without any visible change in structure in the male pronuclei. The female pronuclei are formed immediately following the throwing off of the second polar cell. Each pronucleus enters a definite interkinetic diffuse stage before fusion occurs and discrete chromosomes do not reappear until after the first cleavage nucleus is well established.

Metaphase plates of the zygotes show that two types are present, one containing eleven dyad chromosomes, and the other possessing twelve. There is no evidence of any diminution process going on, the soma cell division being exactly similar to a propagation cell mitosis. The soma cellsoften do not contain more than the diploid number of chromosomes. and in such cases the chromosomes are all dyad in structure. In a few cases somatic cells were found in which there were varying numbers of chromosomes, some of which were apparently dyad in structure while the others were smaller and were monads. In no such case did the chromosome number pass beyond that of double the diploid number, i. e., twenty-four. In nuclei located in the intestinal wall of

the adults several mitotic divisions were observed in which the chromosome number was definitely twenty-four, and no appearance of any type of constriction could be recognized.

Study of gametogenesis shows that the diploid number of chromosomes is twelve and the haploid number is six. The spermatozoa contain five and six chromosomes and the ova six. The autosomes, prior to the first division, are di-tetrads in structure while the idiochromosome is tetrad; after maturation is completed all chromosomes are dyads, and in the soma cells they have some tendency to further separate into a monad condition, particularly in the intestinal wall cells. The chromosomes of the germ cells are therefore compound bodies, each equivalent to two somatic chromosomes, but bodies in which the union of these two has become so well established that it is the exception rather than the rule for this plane of joining to break down, even in the soma cells. Some chromosomes are apparently more firmly joined than others for only in a very few cases were all found to have been split up, the majority of cells showing this phenomenon of division having some, but not all, of the chromosomes involved in the process. No diminution process occurs. No evidence of the isolation of the idiochromosome in a separate karyosome during interkinesis was found among the spermatogonia or any stage in oogenesis, but such separate existance was definitely noted in the spermatocytes and the spermatozoa, though it apparently fuses with the other chromatic material during the metamorphosis of the spermatid.

E. Trichinelloidea.

1. Trichinellidae.

Trichosomoidinae.

a) *Trichosomoides crassicauda* (Bellingham) Railliet. From the urinary bladder of *Epimys norvegicus.*

Syn: *Trichocephalus crassicauda* (Bell.) Elberth,
Trichodes crassicauda (Bell.) von Linstow,
Trichosoma crassicauda Bellingham,
Trichosoma crassicauda specifica Loewenstein,
Trichosoma muris decumani Rayer (in part),
Trichosomum crassicaudum (Bell.) Creplin.

The gametogenesis of *T. crassicauda* is very difficult to work out owing to the extreme minuteness of the germ cells and the presence of the parasitic male in the uterus of the female. One's efforts are well repaid, however, by the finding in the soma cells of clear-cut "V"-shaped chromosomes that rival the diagrams of text-books in their simplicity and behavior. They are reminiscent of the chromosomes of *Ascaris megalocephala* in their shape, and also like those of that animal

in that they lose their rod-shaped form and clump up into tetrad-like bodies during the maturation divisions. So far as the writer is aware, this is the first instance of this type of chromosome being recorded from Nematodes other than *A. megalocephala*.

Study of the spermatogonia was impossible, the closely crowded cells being so small that even in 2 μ sections with a $^1/_{12}$ oil immersion objective and a No. 12 compensating ocular they appeared as small dots thickly overlaid one on the other.

The late primary spermatocytes were the first cells of sufficient size and definition to be accurately observed. Here were found present in the nuclei four small tetrad-like chromosomes (fig. 111) that evidently represented the reduced number. These bodies were too minute to distinguish whether there was more than one longitudinal constriction present at this time (fig. 112). The first division was clearly due to a longitudinal splitting of three of these bodies, the fourth one passing undivided to one of the daughter nuclei.

Careful examination showed that the chromosomes of the secondary spermatocytes were again tetrad in form. Whether this is due to a secondary longitudinal split or because the original structure contained two such clefts could not be determined by observation. It seems more probable that the latter is the case inasmuch as the heterochromosome — X type, with X equaling one — was tetrad during the first prophase and passed undivided to one of the secondary spermatocytes. Its longitudinal cleft represented the plane of the second division and it would be quite likely that a similar indication of the future plane of this same division should be present in the autosomes as well as in the heterochromosome.

The two types of secondary spermatocytes (fig. 113, 114) reduce to spermatids by a second longitudinal division of the chromosomes, one containing three dyad autosomes and the other three dyad autosomes and one dyad idiochromosome.

The spermatozoa are peculiar in form, resembling in shape and motion a type intermediate between the usual amoeboid cells of the Nematodes and the flagellated forms of many other groups. There is an active change in shape of the head region as well as a definite movement of the whip-like tail, especially after the spermatozoa are set free in the uterus.

In the oogonial mitotic figures, eight minute rod-shaped bodies, usually bent in the shape of a "V", are clearly distinguishable. A slight constriction at the point of the "V" is interpreted to be the Querkerbe, being in every respect similar to the conditions found in *Lepidosiren* (Rom, 1911).

After the reorganization of the chromatic materials during the first maturation prophase, eight definitely dyad chromosomes appear which pair and form four di-tetrad bodies by reason of the possession of the Querkerbe and a longitudinal cleft in addition to that left by the fusion plane.

The metaphase plate contains four di-tetrad chromosomes (fig. 117) which undergo longitudinal division and give rise to a secondary oocyte with four tetrad chromosomes (fig. 118).

The second division is also longitudinal, the resultant ovum receiving four dyad chromosomes. The nucleus undergoes reorganization, but the chromosomes reappear in the same form. The female pronucleus therefore contains four dyad chromosomes, dumb-bell in shape.

The two pronuclei fuse and during the early prophase of the first cleavage division the chromosomes undergo a distinct change of form, assuming the "V" shape again and characterized by the possession of the apically placed Querkerbe noted in the oogonial chromosomes. The "V" shape is perhaps due to the weakening of the chromosome at the middle because of the presence of the constricted area of the Querkerbe.

A diminution phenomenon was not found to be present, the somatic chromosomes never assuming the monad condition.

V. Discussion.

The study of the events of gametogenesis in the twelve hitherto unexamined species of Nematodes, as well as additional information concerning four fairly well described species, has brought to light considerable evidence concerning: 1. the nature and meaning of the presence of di-tetrad chromosomes; 2. the Querkerbe; 3. the type and number of the heterochromosomes; 4. the behavior of this body; 5. the universality of the "diminution" phenomenon; and 6. some evidence regarding the relation of chromosome number and type to the systematic position of the various species.

1. In most animals and plants it is supposed that the diploid chromosomes are of the simplest possible structure, i. e., they are monads, and during maturation they undergo a synaptic union of pairs — usually parasynapsis —, and also show a longitudinal split which may appear either before or after the pairing occurs. These planes of longitudinal splitting and of parasynapsis respectively indicate the planes of the future homeotypic and heterotypic divisions. This four-parted body has been termed a "tetrad".

The term "di-tetrad" is applied to a chromosome which is composed of eight units, each of which fundamentally is an independant unit, and is employed in place of "octad" because a study of the formation

of a typical eight-parted chromosome shows that it is not formed by the close union of eight parts into a common whole (that is, involving synmixis), but is the result of a loose joining of two "tetrads" by a process of pseudo-reduction, and in reality is two semi-independent tetrads rather than a compact eight-parted structure.

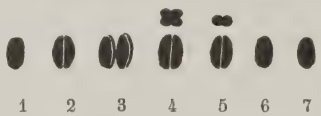
The di-tetrad chromosome, either in structure or in potential, is of wider distribution among Nematodes than is commonly realized. This form of chromosome is found only in the haploid number and occurs just preceeding the first maturation division. The diploid chromosomes in such cases are always dyads, and as such are found in the nucleus of the zygote. They often retain their dyad condition in the germ cells throughout the whole life cycle, though in some cases they may further divide and appear as tetraploid in number and monad in structure. In the embryonic soma cells, whether diminution occurs or not, the dyad chromosomes, in whole or in part, in most cases gradually undergo a final division into the tetraploid number of monad bodies. In the somatic cells of the adult this process is shown at its height.

As a tendency to combine the chromosome into larger units appears in the germ cells, the first step in the process is the fusion of two somatic chromosomes to form a dyad body, and such a body is first found in the germ cells of that animal. The plane of this union is indicated by a constriction which HÄCKER (1895, p. 586) has called the *Querkerbe*. The diploid chromosomes thus become dyad in structure. During Prophase I a longitudinal split occurs in each dyad chromosome, thus forming a tetrad body. By parasyndesis these tetrads unite into pairs which thus become di-tetrads. The plane of the first maturation division passes through one of the longitudinal splits formed by the clefts of the original tetrads or through the plane of syndesis. If through the latter plane, the division is reductional, if through the former, the division is equational. In *Toxascaris canis* the first division is apparently equational. The resulting chromosomes are tetrads. In a few cases, *Acuaria spiralis* for example, the original longitudinal split is obscured until after the first division, thus explaining the appearence of "tetrad" chromosomes before each maturation division. In some Nematodes and some mammals the chromosomes show only as tetrads in Prophase I and then undergo a second pairing, again forming tetrads in Prophase II. Other forms show two tetrads closely allied, but not actually fused, before the first division occurs. However the details of the method, the chromosomes entering the second maturation divisions in all of these cases are morphologically four-parted, these parts being more or less loosely connected into a single unit, the "tetrad". The second division follows and reduces the tetrads to dyads. The mature germ cells thus contain dyad chromosomes and hence the zygote also contains

dyads, here in the diploid number. These chromosomes may retain their dyad structure in the germ cells. In *Toxascaris canis* the Querkerbe disappears, but as no division occurs, the number of chromosomes remains diploid. In some species the germ cell chromosomes divide along the plane of the Querkerbe, the primordial germ cells showing the tetraploid number of monad bodies. The somatic cells consistantly show this reduction to the monad condition and the tetraploid number. There are a few forms in which all of the chromosomes do not separate into their component parts, viz., *Physaloptera turgida*. The culmination of such a series is found in *Protospirura muris*, where the dyad condition is maintained throughout the life cycle of both germinal and somatic cells as the simplest morphological form of the chromosomes.

Text-figure A, shows a typical chromosome cycle of a tetrad type of chromosome and text-figure B of five types of di-tetrad chromosomes, illustrating the steps in the formation and division of these various forms of chromosome in various Nematode species.

The position of forms such as *Belascaris mystax* in this series is doubtful; two different interpretations being about equally possible.



1 2 3 4 5 6 7

Fig. A. Diagrammatic cycle of a tetrad chromosome from sex cells of *Belascaris mystax*. 1. Monad form found in primordial germ cells. 2. Dyad form found in early Prophase I. 3. Parasyndesis of two dyads — late Prophase I. 4. Tetrad form found in Metaphase I. 5. Dyad form found in Metaphase II. 6. Monad form found in matured germ cells and in zygote. 7. Monad form found in embryonic propagation and soma cells.

This species possesses a monad condition of the diploid chromosomes and a tetrad condition of the haploid. Such a condition may be explained on the basis of simplicity, the diploid chromosomes being already reduced to the simplest possible morphological structure. From such a type the more complex di-tetrad forms must have originated. On the other hand, *Protospirura muris* shows a dyad condition in all cells as the unit of structure. *Toxascaris canis* shows that the Querkerbe may be suppressed during certain phases of the cycle, although the chromosomes are actually dyads. *B. mystax* may illustrate a condition in which the dyad form is retained throughout the life cycle, and the Querkerbe has been suppressed, not only in some phases, but throughout the entire history of the chromosomes. The writer is inclined to accept the first interpretation as the more logical because of information available from another angle. *Ascaris lumbricoides* is undoubtedly a type in which the somatic chromosomes are monads that do not possess a suppressed Querkerbe. These monads are derived by a diminution

process in which each germinal chromosome is accurately split into three bodies, one of which is retained as the somatic chromosome and the other two are eliminated into the cytoplasm. *Belascaris mystax* possesses germinal and somatic chromosomes entirely similar to those of *A. lumbricoides*, and also undergoes a diminution division. In this case, however, the amount of eliminated chromatin is not definitely arranged into any certain number of bodies. From this standpoint it seems that *B. mystax* is midway between *A. lumbricoides* and forms such as *T. canis* in which the somatic chromosomes are tetraploid in number and in which the chromatin lost by diminution fails to be organized into distinct, countable units. From this aspect, *B. mystax* should be considered as more simple cytologically than *T. canis* and more complex than *A. lumbricoides*, thus favoring the interpretation of an actual monad condition in its diploid chromosomes rather than that of an apparent monad formed from a true dyad by the external disappearance of the Querkerbe.

The next step, at least along one line, is shown by the varieties of *Ascaris megalocephala*. In these forms the germinal chromosomes are equivalent, not only to two somatic chromosomes and a certain amount of eliminated chromatin, but in the case of *A. meg. biv.*, to twenty-two such chromosomes, and in *A. meg. univ.*, to twenty-six, plus the chromatin lost at diminution. Instead of each heterochromosome being equivalent to two somatic chromosomes, it forms eight such bodies in each variety of this species.

The haploid chromosomes of *A. megalocephala* itolis have been shown by BLANCKERTZ (1910) to be tri-tetrads (12-parted) with a possibility that each visible portion has undergone two longitudinal splits before entering the compound body. This would account for twelve of the twenty-six somatic elements that are formed by the dissociation of the germ cell chromosome. This observation has not been substantiated by later workers so can only be regarded as suggestive and not as conclusive in its indications.

2. The Querkerbe, as already stated, is a term introduced by HÄCKER in 1895 to indicate a transverse constriction of a chromosome. HÄCKER and his students maintained that this transverse constriction is the forerunner of a maturation division and HÄCKER (1911) states that its appearance is a proof of metasyndesis (telosyndesis). AGAR (1911) and KORNHAUSER (1915) have both shown that the Querkerbe found in the chromosomes of copepods, nematodes, molluscs and some vertebrates, can not be taken for proof of either para- or telosyndesis. The Querkerbe is never a definite forerunner of a future maturation division. Earlier work on *Toxascaris canis* led the writer to advance two interpretations of this phenomenon. The first stated that the Querkerbe

was an accidental structure, a meaningless constriction that might be the forerunner of fragmentation processes such as HANCE (1917) has shown so clearly as occurring in the somatic chromosomes of the pig. The second was that the presence of the Querkerbe was the definite indication of a plane of division of each "soma" cell chromosome into

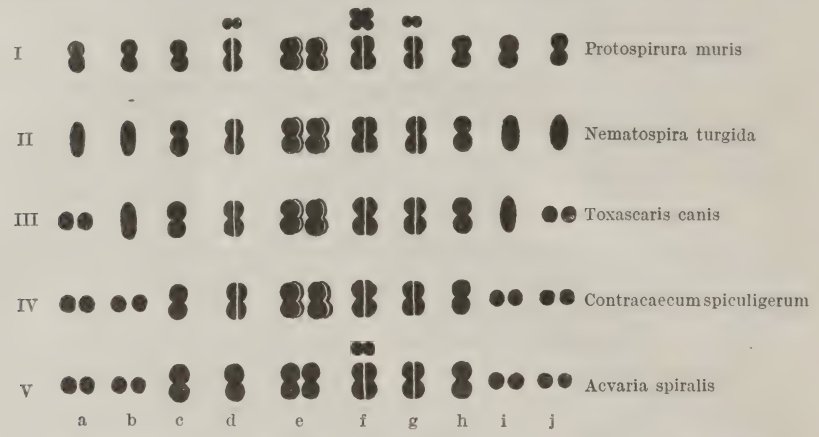


Fig. B. Diagrammatic cycle of octad (di-tetrad) chromosomes from sex cells of various Nematodes.

		I Protospirura muris	II Nematospira turgida	III Toxascaris canis	IV Contracaecum spiculigerum	V Acuaria spiralis
a.	From soma cells of adult	dyad	dyad, Querkerbe suppressed	true monads	monads	monads
b.	From primordial germ cells	dyad	dyad, Querkerbe suppressed	dyad, Querkerbe suppressed	monads	monads
c.	From early Prophase I.	dyad	dyad	dyad	dyad	dyad
d.	From mid Prophase I.	tetrad	tetrad	tetrad	tetrad	dyad
e.	From late Prophase I.	tetrad fusion	tetrad fusion	tetrad fusion	tetrad fusion	dyad fusion
f.	From Metaphase I.	di-tetrad	di-tetrad	di-tetrad	di-tetrad	tetrad
g.	From Metaphase II.	tetrad	tetrad	tetrad	tetrad	tetrad
h.	From mature germ cells and zygote	dyad	dyad	dyad	dyad	dyad
i.	From propagation cells	dyad	dyad, Querkerbe suppressed	dyad, Querkerbe suppressed	monads	monads
j.	From embryonic soma cells	dyad	dyad, Querkerbe suppressed	monads	monads	monads

two somatic chromosomes, i. e., a chromosome possessing this body was plurivalent, and therefore as it is consistently present only in the sex cell chromosomes, these bodies are equivalent to at least two somatic chromosomes. The latter theory at that time was deemed as of minor import since plurivalent chromosomes and diminution divisions were not known in all cases where the Querkerbe was found. Recent work

has shown that the diminution phenomenon is quite restricted in range and has no connection at all with the formation of somatic chromosomes as far as number is concerned. The work in this paper has shown that the Querkerbe has been present in every case of plurivalent chromosomes examined and that the presence or absence of diminution was purely incidental and of no import from the aspect of numbers of chromosomes. It has also been shown that the plurivalent condition may be of varying degrees, expressing itself by the reduction of dyads to monads in none, some, or all of the somatic chromosomes and gradually increasing in range to include all of the chromosomes of the primordial germ cells. The amount of breaking up is perhaps indicative of the phylogenetic development of the process, the less the dyad condition reverts to a simple monad form, the more specialized the cytological content of the species, and the stronger the bond between the fused elements of the germinal chromosomes. As this fusion becomes absolute, its visible indicator — the Querkerbe — may also disappear. The culmination of such a series would be found in *Ascaris megalocephala* where each germinal chromosome is undoubtedly plurivalent yet the fusion has progressed so far that all traces of it are lost to view in the chromosomes of the sex cells. One must be careful in his interpretation of a structure as a true Querkerbe not to confuse it with the constrictions such as are described by Hance (1917). In fragmentation, there is no definite number into which the chromosomes divide, and the phenomenon is restricted to somatic cells. In a true plurivalent condition — Querkerbe present — the number of chromosomes formed by this action is always constant for any one species and is not necessarily confined to the somatic cells, showing it to be a regular and deep-seated phenomenon.

The interpretation of the true Querkerbe as being indicative of the presence of a plurivalent condition of the diploid chromosomes of the sexual cells is therefore again presented with what is believed to be definite evidence of its existence, at least among Nematodes. The writer is inclined to accept the same interpretation for the Querkerbe of molluscs and copepods as reduction to a tetraploid monad condition is found in the soma cells of some species of these groups. The writer is also inclined to doubt the presence of a true Querkerbe among the vertebrates, at least as far as present studies indicate, and suggests that the structure there noted is a case of constriction preceeding ordinary somatic chromosome fragmentation, and not one of a plurivalent chromosome indicating the plane by which it may reduce to its component elements.

3. In each of the sixteen species studied the presence of a heterochromosome complex was established. This group usually consisted of only one member, though numbers as high as six were found in one form,

and were generally independent of any connection to the autosomes. In one species a non-visible bond seemed to occur between the heterochromosome and an autosome (*Physaloptera turgida*), in another (*Belascaris mystax*) the heterochromosome was visibly attached to one autosome, and in *Ascaris megalocephala* the heterochromosome was fused so closely to an autosome that it could only occasionally be identified.

Study of the literature shows that only one authenticated occurrence of a "Y" chromosome among Nematodes has been described (GOODRICH, 1916, for *Ascaris incurva*). In this case the "Y" was paired with eight "X" chromosomes. In all other instances, and this includes the species described in this paper, the heterochromosomes have been of the "X" type only. The following table (Table III) shows the numbers included in the heterochromosome complex of the species studied at this time.

4. The behavior of the heterochromosome complex was carefully followed out, giving several interesting results.

a) The heterochromosomes first divide at the second maturation division as a general rule.

Table III.

Name	Heterochromosome number	Condition	Somatic equivalents
Acuaria spiralis	X = 1	free	2
Ascaris megalocephala bivalens	X = 1	attached	8
Ascaris megalocephala univalens	X = 1	attached	8
Belascaris mystax	X = 1	attached	1
Contracaecum spiculigerum	X = 1	free	2
Cruzia tentaculata	X = 1	free	2
Heterakis papillosa	X = 1	free	2
Nematospira turgida	X = 1	free	2
Physaloptera turgida	X = 1	free [1]	2
Protospirura muris	X = 1	free	1 [2]
Syphacia obvelata	X = 1	free	1
Trichosomoides crassicauda	X = 1	free	2
Belascaris triquetra	X = 2	free	2
Ganguleterakis spumosa	X = 2	free	2
Ascaris lumbricoides	X = 5	free	1
Toxascaris canis	X = 6	free	2

[1] Non-visible bond exists between heterochromosome and an autosome.
[2] Somatic chromosomes are dyad in structure.

b) A wide range of behavior in relation to association of heterochromosome and autosome chromatic material in various phases of the chromosome cycle was observed. In *Belascaris triquetra* the heterochromosome material forms a separate karyosome at every interkinetic

period of both spermatogenesis and oogenesis, never at any time mixing closely with that of the autosomes. Similar conditions have been reported for *Heterakis dispar*, *H. inflexa*, and *H. vesicularis* by Gulick (1911).

In *Toxascaris canis* a separate karyosome for the heterochromosome material is found only in spermatogenesis. During oogenesis there is no apparent separation of the chromatic material of the interkinetic periods into autosome and heterochromosome.

Nematospira turgida furnishes an example of a form in which the heterochromosome does not enter the diffused spireme stage of the autosomes during maturation, but does so at other times in the germ cycle. During all of the divisions of the primordial germ cells, from the time of their first isolation in the embryo until the last gonial division, the heterochromosomes are indistinguishable from the autosomes except while in the form of discrete chromosomes.

In *Physaloptera turgida* the heterochromosome is indistinguishable except while in the form of a discrete chromosome, yet is in such close physiological association with one autosome that, although the bond between the two is not visible, the latter is much delayed during the maturation divisions of both male and female germ cells. This autosome might easily be confused with a second "X" chromosome were it not for the fact that it divides at both maturation mitoses while the true "X" chromosome does not. A possible interpretation of this chromosome as an "X- Y" body, separating at the first division and each dividing at the second, forming, with the "X" element, a heterochromosome complex of the "X=2, and Y=1" type, must not be overlooked, but the possibility does not seem probable in the light of other factors which need not be considered at this time.

The heterochromosome of *Belascaris mystax* is closely fused to the end of an autosome, but the point of fusion is marked by a definite constriction and can be detected in both male and female germ cells.

The culmination of the series is found in *Ascaris megalocephala*. Here the fusion of the heterochromosomes to the autosomes is so complete that only in extremely isolated instances can their presence be distinguished. In these cases the heterochromosomes have failed to unite with an autosome in the formation of the compound germ-cell chromosomes from the numerous small monad somatic bodies, and their fate can be determined accurately. In such cases as these a definite measurable decrease in the length of the autosomes is present (Montgomery, 1908). The heterochromosomes are consistently isolated however, in separate karyosomes during interkinesis of the somatic cells (Geinitz, 1915).

5. Since the description of the diminution process in *Ascaris megalocephala* by Boveri, zur Strassen, Bonnevie and others, the meaning and distribution of this phenomenon has been discussed by numerous authors. Meyer (1895) reported it in *Ascaris labiata*, *A. lumbricoides* and *A. rubicunda*; Walton (1918) in *Toxascaris canis*; and Goodrich (1916) for *Contracaecum incurvum*, the only non-ascarid thus far to be reported. There has been no instances of its occurence in other than members of the *Ascaridae*, and with the exception of *Contracaecum incurvum*, in other than members of the *Ascarinae*. It has been shown in this paper that the same narrow distribution limits have been maintained, and in addition has shown that others of the genus *Contracaecum* fail to show this phenomenon. Until further work has fully established the systematic position of the form reported by Goodrich — even now in some dispute —, the apparent exception to the narrow limitations of diminution presence can not be considered other than of minor import. Of the sixteen forms studied and reported in this paper, seven belong to the *Ascaridae* and six of these are in the sub-family *Ascarinae*. These six, but none of the other ten, each showed a well developed diminution process in the somatic divisions of the early embryonic development.

The accompanying Table IV records the Nematodes now known to show this phenomenon and the observers first reporting them.

Table IV.

Family	Name	Authority
Ascaridae (*Ascarinae*)	*Ascaris labiata*	Meyer, 1895
	Ascaris lumbricoides	Meyer, 1895
	Ascaris megalocephala bivalens	Boveri, 1892
	Ascaris megalocephala univalens	Boveri, 1892
	Ascaris rubicunda	Meyer, 1895
	Belascaris mystax	new
	Belascaris triquetra	new
	Toxascaris canis	Walton, 1918
(*Anisakinae*)	*Contracaecum incurvum*	Goodrich, 1916

The meaning of the process has not yet been satisfactorily explained, although the idea of it as a means of elimination of the excess of metabolism in a growing embryo is probably a step in the right direction. It is noticable however, that the process is most marked in forms in which the zygote chromosomes are the most compact and in which the metabolic rate is correspondingly greater. *Ascaris megalocephala* furnishes the best example of this type, the zygotic chromosomes being compacts oftwenty-two to twenty-six body-cell equivalents, the metabolic action being correspondingly concentrated, and the accompanying "excess chromatin" of the first "soma cell" division being especially noticeble.

That the process may be related to the activities of the sex chromosomes is indicated by the fact that in every case where diminution has been reported, the heterochromosome has been multiple, either as to number or as to equivalence to somatic chromosomes.

Whatever the meaning may actually be, diminution is found only in the more highly specialized members of the most specialized family of the parasitic Nematodes. Since this group is composed of degenerate forms, specialization means increased degeneration and diminution may be but a visible sign of senescence within the cells themselves of These decadent forms.

6. The relation between the cytological structures and the taxonomic position of the worms studied is interesting in that several peculiar coincidences of chromosome number and behavior are correlated with certain groups of worms.

The first of these has been mentioned above. The phenomenon of diminution is probably restricted to worms of the sub-family *Ascarinae* and has been found in every species of this group which has been examined from the standpoint of studying early cleavage processes.

Another curious correlation is that the number of heterochromosomes of the "X" type present is always *one* in all of the Nematode superfamilies except the *Ascaroidea*, and with but one exception — *Ganguleterakis spumosa* —, only members of the family *Ascaridae* and the sub-family *Ascarinae* have been shown to possess more than one such body. Morphologically Ganguleterakis has been shown to be a connecting link between the *Ascaridae* and the *Heterakidae* and now the cytological evidence points to the same conclusion. A "Y" chromosome has been reported, or suggested as a possibility, for several widely separated forms. *Angiostomum nigrovenosum*, *Ascaris mystax* (sp. *canis*), *Contracaecum incurvum*, *Physaloptera turgida*, *Rhabditis aberrans* and *Strongylus filaria* have all been reported as possibly showing such a chromosome, but only in *C. incurvum* has the presence been verified by other workers.

Study of the literature shows a peculiar consistency in chromosome numbers among the members of various genera other than *Ascaris*. *Heterakis* consistently shows five chromosomes as the haploid number, *Rhabditis* seven, *Sclerostomum* six and *Strongylus* six.

Morphologically, these genera are quite distinct within themselves, few, if any, aberrant forms being included. The members of any one genus are closely related, hence it is not surprising that their cytological content should also be characteristically similar. On the other hand, *Ascaris* is a group comprised of a very heterogeneous collection of forms which are more or less similar only in minor respects, and is constantly being reduced in size by the establishment of new genera and even

families based on close morphological unity of certain species. In harmony with this heterogeneous condition of the group from a taxonomic aspect, it is not surprising to find great diversity among chromosome numbers and behavior. The haploid chromosomes of the forms which have thus far been examined vary in number from one in *Ascaris megalocephala univalens* to twenty-four in *A. lumbricoides*, and the somatic number from sixteen in a dog Ascarid (Carnoy, 1887 b) to one hundred and four in *A. megalocephala bivalens*. The heterochromosome number also varies from one in forms like *A. megalocephala*, to five in *A. lumbricoides*.

The above mentioned correlations are of such outstanding constancy that they may well be useful as additional information in the study of the systematic position of Nematode species, particularly so among forms in which the structural criteria are often very indefinite.

VI. Summary.

The work recorded in this paper has been based on a greater number of species than has that of any other work in the field of Nematode Cytology and the results have a correspondingly wider application and a greater degree of accuracy because of this wide range of the material available.

The sixteen species studied represented twelve genera, ten subfamilies, eight families and five super-families of the order Nematoda. The accompanying table (Table V) gives the present status of the classification of the parasites and also includes the list of Hosts from which the material studied was obtained.

In one case a new genus and species — *Nematospira turgida* — were established. *Acuaria spiralis*, *Cruzia tentaculata* and *Syphacia obvelata* were found in new hosts and several forms were reported from new localities. The material of *Belascaris triquetra* used was taken from a dog, the usual host animals for this parasite being lions, wolves and bears. The dog, however, has long been known to be an occasional host to this form.

The following is a brief summary of the results gained by a study of sixteen species. The members of the *Ascarinae* are described first because of their apparently greater specialization and further removal from the primitive Nematode condition.

1. *Ascaris lumbricoides*. The haploid number consists of twenty-four chromosomes in the females. One-half of the males possess nineteen tetrad autosomes, the other half nineteen tetrad autosomes and five dyad heterochromosomes. The heterochromosome complex of five members is of the X type. The diploid number is forty-three in the males and forty-eight in the females, all monads in structure. One of

the heterochromosome members is consistently larger than its mates. The diploid chromosomes are each equivalent to three bodies, two of which are lost at diminution and the third remains as the somatic chromosome. The heterochromosome complex does not form a separate karyosome during interkinesis in either spermatogenesis or oogenesis.

2. *Ascaris megalocephala bivalens.* The germ cell chromosomes were determined to each be equivalent to twenty-two somatic elements. The attached X chromosome is equivalent to eight somatic bodies.

Table V.

Super-family	Family	Genus	Species	Host
Ascaroidea	*Ascaridae* (*Ascarinae*)	*Ascaris*	*lumbricoides*	Pig
			megalocephala biv.	Horse
			megalocephala univ.	Horse
		Belascaris	*mystax*	Cat
			triquetra	Dog
		Toxascaris	*canis*	Dog
	Ascaridae (*Anisakinae*)	*Contracaecum*	*spiculigerum*	Pelican
	Heterakidae	*Ganguleterakis*	*spumosa*	Rat
		Heterakis	*papillosa*	Chicken
Filaroidea	*Acuariidae* (*Acuariinae*)	*Acuaria*	*spiralis*	Grackle
	Acuariidae (*Physalopterinae*)	*Physaloptera*	*turgida*	Opossum
	Spiruridae	*Protospirura*	*muris*	Rat
Oxyuroidea	*Cruzidae*	*Cruzia*	*tentaculata*	Opossum
	Oxyuridae	*Syphacia*	*obvelata*	Rat
Strongyloidea	*Trichostrongylidae*	*Nematospira*	*turgida*	Mouse
Trichinelloidea	*Trichinellidae*	*Trichosomoides*	*crassicauda*	Rat

The somatic number of chromosomes is ninety-six or one hundred and four, depending upon the sex of the worm studied.

3. *Ascaris megalocephala univalens.* The germ cell chromosomes were determined to each be equivalent to twenty-six somatic elements. The attached X chromosome is equivalent to eight somatic bodies. The somatic number of chromosomes is fifty-two or sixty, depending upon the sex of the worm studied.

4. *Belascaris mystax.* The haploid number consists of nine chromosomes in each sex. Eight of these are tetrads and one hexad — tetrad autosome plus dyad heterochromosome. The single heterochromosome is of the X type and is normally attached to the end of an autosome. The diploid number of chromosomes is eighteen, all monads. The

diploid chromosomes are morphologically simple, the somatic cells showing the same number and structure of the chromosomes as do the germ cells. The diminution process occurs at the first division of each soma cell after its separation from the propagation cells. The idiochromosome forms a separate karyosome during the interkinetic periods of spermatogenesis.

5. *Belascaris triquetra*. The haploid number consists of twelve di-tetrad chromosomes in the females. One-half of the males possess ten di-tetrad autosomes and the other half ten di-tetrad autosomes and two tetrad heterochromosomes. The heterochromosome complex consists of two X bodies. The diploid number of chromosomes is twenty-two for the males and twenty-four for the females, all dyad in structure. The diploid chromosomes are each equivalent to two somatic elements as well as to a small amount of chromatin which is lost by a diminution process. The somatic numbers of chromosomes are forty-four and forty-eight, according to the sex of the worms studied. The heterochromosomes are isolated from the autosomes during both spermatogenesis and oogenesis by the formation of separate karyosomes for each type of chromosome.

6. *Toxascaris canis*. The haploid number consists of eighteen di-tetrad chromosomes in the females. One-half of the males have twelve di-tetrad autosomes and the other half have twelve di-tetrad autosomes and six tetrad heterochromosomes. The latter form a heterochromosome complex of the X type. The diploid number of chromosomes is thirty in the males and thirty-six in the females, all of them dyads. The diploid chromosomes are each equivalent to two somatic chromosomes, and in addition, to a small amount of chromatin lost at diminution. The somatic number of chromosomes is sixty and seventy-two, all being monad in structure. The heterochromosomes form independent karyosomes during interkinetic periods of the male germ cycle.

7. *Contracaecum spiculigerum*. The haploid number consists of five di-tetrad chromosomes in the femele. One-half of the males possess four di-tetrad autosomes and the other half four di-tetrad autosomes and a tetrad heterochromosome of the X type. The diploid number of chromosomes is nine in the males and ten in the females, all dyads in structure. The diploid chromosomes are each equivalent to two somatic chromosomes. These germ cell chromosomes also reduce to a tetraploid number in the primordial sex cells. The tetraploid number is eighteen and twenty, all monads in structure. A diminution division does not occur. The heterochromosome is not isolated from the autosomes during interkinesis by the establishment of a separate karyosome.

8. *Ganguleterakis spumosa*. The haploid number consists of six tetrad-like chromosomes in the female. One-half of the males possess

four tetrad autosomes, and the other half possess four tetrad autosomes and two tetrad heterochromosomes of the X type. The autosomes are potentially di-tetrads in that they again show a tetrad formation after the first maturation division is completed. The diploid number of chromosomes is ten in the males and twelve in the females, all dyad in structure. The diploid chromosomes are each equivalent to two somatic chromosomes. A diminution process does not occur. The primordial germ cells as well as the somatic cells show a tetraploid number of twenty and twenty-four monad chromosomes. The heterochromosomes are not isolated from the autosomes by the establishment of separate karyosomes during either spermatogenesis or oogenesis.

9. *Heterakis papillosa*. The haploid number consists of five di-tetrad chromosomes in the female. One-half of the males possess four di-tetrad autosomes and the other half four di-tetrad autosomes and a tetrad heterochromosome of the X type. The diploid number of chromosomes is nine in the males and ten in the females, all dyads in structure. The diploid chromosomes are each equivalent to two somatic chromosomes. The germ cell chromosomes also reduce to a tetraploid number in the primordial sex cells. This tetraploid number is eighteen or twenty according to the sex, and each chromosome is monad ni form. A diminution process was not observed. The heterochromosome is isolated from the autosomes during the interkinetic periods of spermatogenesis by the establishment of a separate karyosome.

10. *Acuaria spiralis*. The haploid number consists of six tetrad-like chromosomes in the female. One-half of the males have five tetrad-like autosomes and the other half have six such bodies, one of them being a tetrad heterochromosome of the X type. These autosomes are physiologically di-tetrads, but the second longitudinal split fails to become manifest until after the first division has been completed. The diploid number is eleven for the males and twelve for the females. The diploid chromosomes are each equivalent to two somatic chromosomes. The primordial germ cells as well as the somatic cells have a tendency to show the tetraploid numbers of twenty-two and twenty-four monad chromosomes. A diminution process is not present during somatic mitoses. The heterochromosome forms an individual karyosome during the interkinetic periods of spermatogenesis but not of oogenesis.

11. *Physaloptera turgida*. The haploid number consists of five tetrad chromosomes in the females. One-half of the males show four tetrad autosomes, and the other half four tetrad autosomes and a tetrad heterochromosome of the X type. The autosomes again appear as tetrads before the second maturation division by the formation of a second longitudinal cleft. The diploid number of chromosomes is nine

for the males and ten for the females, all dyads in structure. The diploid chromosomes are each physiologically equivalent to two somatic chromosomes although the soma cells only rarely show the tetraploid number of eighteen or twenty monads. No traces of a diminution phenomenon were observed. The heterochromosome not only does not form a separate karyosome in resting nuclei, but is so closely related to an autosome that the latter is much delayed in division, both in spermatogenesis and in oogenesis.

12. *Protospirura muris.* The haploid number consists of five di-tetrad chromosomes in the females. One-half of the males possess four di-tetrad autosomes and the other half possess four di-tetrad autosomes and a tetrad heterochromosome of the X type. The diploid number of chromosomes is nine for the males and ten for the females. The diploid chromosomes are each equivalent to one somatic chromosome. Neither the somatic cells nor the primordial germ cells have any tendency to show a tetraploid number of monad chromosomes, but retained their dyad structure and diploid number throughout the life cycle. There is no evidence of a diminution process and no tendency for the heterochromosome to form a separate karyosome at any time.

13. *Cruzia tentaculata.* The haploid number consists of six di-tetrad chromosomes for the females. One-half of the males have five di-tetrad autosomes and the other half have five di-tetrad autosomes and a tetrad heterochromosome of the X type. The diploid chromosomes are each equivalent to two somatic chromosomes. Diminution probably does not occur. The primordial germ cells as well as the somatic cells show the tetraploid number of twenty-two and twenty-four monad chromosomes. The heterochromosome is not isolated from the autosomes by the formation of a separate karyosome during the interkinetic periods of spermatogenesis.

14. *Syphacia obvelata.* The haploid number consists of eight tetrad chromosomes in the female. One-half of the males show seven tetrad autosomes, and the other half show seven tetrad autosomes and one dyad heterochromosome of the X type. The diploid number is fifteen for the males and sixteen for the females, all monads in structure. The germ-cell and the somatic-cell chromosomes are morphologically equivalent. There is no isolation of the heterochromosome at any period through the formation of separate karyosomes and there is no evidence of any diminution process.

15. *Nematospira turgida.* The haploid number consists of six di-tetrad chromosomes in the females. One-half of the males show five di-tetrad autosomes and the other half five di-tetrad autosomes and a single heterochromosome of the X type. The diploid number is eleven for the males and twelve for the females, all dyads in structure. The

diploid chromosomes are morphologically equivalent to two somatic chromosomes although the soma cells but rarely show a reduction to the tetraploid number of monad chromosomes. No traces of a diminution process were observed. The idiochromosome maintains its distinct form during meiosis, but apparently fuses with the other chromatic material during the balance of the germ cycle.

16. *Trichosomoides crassicauda*. The haploid number consists of four di-tetrad chromosomes in the female. One-half of the males show three di-tetrad autosomes and the other half show three di-tetrad autosomes and a single tetrad heterochromosome of the X type. The diploid number of chromosomes is seven for the males and eight for the females, all dyads in structure. The somatic cell chromosomes as well as those of the germ cells retain their dyad structure throughout the entire life cycle, no evidence of a reduction to a monad condition being found at any stage. Diminution also fails to occur. The heterochromosome does not remain isolated in a separate karyosome during the resting stages of any of the cells. The chromosomes are definitely "V" shaped throughout the germ cycle except during the maturation period. Here they assume the typical di-tetrad form of many of the Nematodes, and reduce through tetrads to dyads before they resume the "V" shape again. The spermatozoa are peculiar in possessing a whip-like tail as well as an amoeboid head. There is no evidence of glycogen storage at any period of the spermatozoon metamorphosis.

The accompanying table (Table VI) sums up the results of the above studies.

Examination of the above results and comparisons with the work of other investigators leads to the postulation of some general statements as regards to *processes*.

1. The presence of di-tetrad haploid chromosomes is an indication that the germ cell chromosomes are compound, each being equivalent to two monad chromosomes such as are usually found in somatic cell nuclei and occasionally in the primordial germ cell nuclei. The Querkerbe of the germ cell chromosomes indicates the point of this union, which may or may not be permanent. When permanent, the chromosomes retain their dyad condition throughout the germ cycle.

2. The development of the compound chromosome in the germ cells of certain of the parasitic Nematodes closely parallels what is known of the phylogeny of these same species from the morphological and other standpoints, thus giving an added criterion in the study of this puzzling group. The following series is correct from both cytological and morphological standpoints as beginning with a less complex form and preceeding to a more complex type. Beginning with *Syphacia obvelata*, the diploid chromosomes are monads like those of the soma

Table VI.

Name	Haploid number of chromosomes	Diploid number of chromosomes	Diminution	Somatic number of chromosomes	Hetero-chromosome number	Autosome Unit Value
Acuaria spiralis	6 (di-tetrads)	11—12 (dyads)	undetermined	22—24	X = 1	2
Ascaris lumbricoides	24 (tetrads)	43—48 (monads)	present	43—48	X = 5	1 + 2
Ascaris megalocephala biv. . .	2 (rod-shaped)	4 (rod-shaped)	present	96—104	X = 1	22 + (X = 8)
Ascaris megalocephala univ. .	1 (rod-shaped)	2 (rod-shaped)	present	52—60	X = 1	26 + (X = 8)
Belascaris mystax	9 (tetrads)	18 (monads)	present	18	X = 1	1 +
Belascaris triquetra.	12 (di-tetrads)	22—24 (dyads)	present	44—48	X = 2	2 +
Contracaecum spiculigerum . .	5 (di-tetrads)	9—10 (dyads)	absent	18—20	X = 1	2
Cruzia tentaculata	6 (di-tetrads)	11—12 (dyads)	undetermined	22—24	X = 1	2
Ganguleterakis spumosa	6 (di-tetrads)	10—12 (dyads)	absent	20—24	X = 2	2
Heterakis papillosa	5 (di-tetrads)	9—10 (dyads)	undetermined	18—20	X = 1	2
Nematospira turgida	6 (di-tetrads)	11—12 (dyads)	absent	22—24	X = 1	2
Physaloptera turgida	5 (tetrads)	9—10 (dyads)	absent	18—20	X = 1	2
Protospirura muris	5 (di-tetrads)	9—10 (dyads)	absent	9—10	X = 1	1 [1]
Syphacia obvelata	8 (tetrads)	15—16 (monads)	absent	15—16	X = 1	1
Toxascaris canis	18 (di-tetrads)	30—36 (dyads)	present	60—72	X = 6	2 +
Trichosomoides crassicauda . .	4 (di-tetrads)	7—8 (dyads)	absent	7—8 [2]	X = 1	2

[1] Somatic chromosomes are dyad in structure.

[2] Somatic chromosomes and primordial germ-cell chromosomes are "V" shaped.

cells — the simple condition. A second stage is found in *Belascaris mystax* and *Acuaria spiralis* where the germ cell chromosomes are equivalent to one somatic chromosome and, in addition, to some chromatin which is lost by diminution. *Ascaris lumbricoides*, in which a germ cell chromosome is equivalent to one somatic chromosome plus two definite bodies lost at diminution, is also in this group of the series, probably rather lower than the other two examples given above. Next comes a number of species in which the haploid chromosomes are di-tetrads, reducing to dyad diploid bodies, each of which is equivalent — either physiologically or morphologically — to two somatic chromosomes. *Toxascaris canis* is an example of this group. The series culminates in such forms as the varieties of *Ascaris megalocephala* in which each germ cell chromosome is equivalent to many somatic elements, in these cases to twenty-two and twenty-six. In these cases the heterochromosomes are also compound, each being equivalent to eight somatic chromosomes. In addition, the autosomes also possess a certain amount of excess chromatin which is eliminated at the diminution division of the soma cells.

3. The presence of the tetraploid — or even higher — number of chromosomes in the soma cells of Nematodes is not an indication of a fragmentation process, but rather indicates the phylogenetically simple number for the species and points to the fact that the germ-cell chromosomes are compounds of a definite number of these simple somatic chromosomes; the Querkerbe, when present, indicating the plane of such fusion. The presence of the tetraploid number of chromosomes in both the somatic cells and in the primordial germ cells points to another line of evidence as to the simplicity or complexity of the species from a phylogenetic standpoint.

4. All of the Nematodes studied showed a heterochromosome complex of the X type, usually one in number, but consisting of two members in *Belascaris triquetra* and *Ganguleterakis spumosa*, five in *Ascaris lumbricoides* and six in *Toxascaris canis*.

5. The relationship of the heterochromosomes to the autosomes is illustrated by a series in which the heterochromosomes are formed from a separate karyosome in both the males and the females — *Belascaris triquetra* —, from a separate karyosome in males only — *Toxascaris canis* —, are distinct from the autosomes only during the maturation division period — *Cruzia tentaculata* —, are physiologically associated with an autosome — *Physaloptera turgida* —, are visibly connected to an autosome — *Belascaris mystax* —, and finally, are attached to an autosome so closely that their presence can not be detected except in isolated instances — *Ascaris megalocephala*. This series is in no way phylogenetic.

6. There is no wide-spread tendency for the isolation of the heterochromosome from autosome material during interkinesis.

7. Diminution is found in all of the *Ascarinae* studied but absent in all the others, with the exception of the very doubtfully classified *Contracaecum incurvum* (*Ascaris incurva*).

VII. Bibliography.

Agar, W. E. (1911): The Spermatogenesis of *Lepidosiren paradoxa*. Quart. journ. of microscop. science, N. S. **57**, 1—44, pl. 1—5, 1 textfig. — Ders. (1912): Transverse Segmentation and Internal Differentiation of Chromosomes. Ebenda. **58**, 285—298, pl. 12—13. — Ders. (1920): Cytology, with Special Reference to the Metazoan Nucleus. London. XII and 124 pp., 91 fig. — Armbruster, L. (1913): Chromosomenverhältnisse bei der Spermatogenese solitärer Apiden (*Osmia cornuta* Latr.). Beiträge zur Geschlechtsbestimmungsfrage und zum Reduktionsproblem. Arch. f. Zellforsch. **11**, 242—326, Taf. 11—13, 10 Fig. — Blanckertz, R. (1910): Die Ausbildung der Tetrade im Ei von *Ascaris megalocephala univalens*. Ebenda **6**, 1—18, Taf. 1—2. — Bonnevie, K. (1902): Über Chromatindiminution bei Nematoden. Jenaische Zeitschr. f. Naturwiss. **36**, 275—288, Taf. 16—17. — Boring, Alice M. (1909): A Small Chromosome in *Ascaris megalocephala*. Arch. f. Zellforsch. **4**, 120—131, Taf. 10. — Boveri, T. (1887): Zellenstudien I. Die Bildung der Richtungskörper bei *Ascaris megalocephala* und *Ascaris lumbricoides*. Jena. 93 S., 4 Taf. — Ders. (1892): Über die Entstehung des Gegensatzes zwischen den Geschlechtszellen und den somatischen Zellen bei *Ascaris megalocephala*. Sitzungsber. d. Ges. f. Morphol. u. Physiol., München. **8**, 114—125, 5 Fig. — Ders. (1909a): Die Blastomerenkerne von *Ascaris meg.* und die Theorie der Chromosomenindividualität. Arch. f. Zellforsch. **3**, 181—268, Taf. 7—11, 7 Fig. — Ders. (1909b): Über „Geschlechtschromosomen" bei Nematoden. Ebenda **4**, 132—141, 2 Fig. — Ders. (1911): Über das Verhalten der Geschlechtschromosomen bei Hermaphroditismus. Beobachtungen an *Rhabditis nigrovenosa*. Verhandl. d. phys.-med. Ges., Würzburg, N. F. **41**, 83—97, 19 Fig. — Braun, H. (1909): Die spezifischen Chromosomenzahlen der einheimischen Arten der Gattung Cyclops. Arch. f. Zellforsch. **3**, 449—482, Taf. 24—25, 2 Fig. — Carnoy, J. B. (1887a): La Cytodiérèse de l'Oeuf chez quelques Nematodes. La cellule **3**, 1—103, pl. 1—8. — Ders. (1887b): Appendice. Les Globules Polaires de l'*Ascaris clavata*. Ebenda **3**, 247—324, pl. 1. — Cutler, D. W. (1918): On the Sterility of Hybrids between the Pheasant and the Gold Campine Fowl. Journ. of genetics **7**, 155—166, pl. 9. — Edwards, C. L. (1910a): The Sex-determining Chromosomes in *Ascaris*. Science, N. S. **31**, 514—515. — Ders. (1910b): The Idiochromosomes in *Ascaris megalocephala* and *Ascaris lumbricoides*. Arch. f. Zellforsch. **5**, 422—429, Taf. 21—22. — Ders. (1911): The Sex-chromosomes in *Ascaris felis*. Ebenda **7**, 309—313, Taf. 28. — Frolowa, S. (1912): Idiochromosomen bei *Ascaris megalocephala bivalens*. Ebenda **9**, 149—167, Taf. 13—14. — Fürst, E. (1898): Über Centrosomen bei *Ascaris megalocephala*. Arch. f. mikroskop. Anat. **52**, 97—133, Taf. 8—9. — Geinitz, B. (1915): Über Abweichungen bei der Eireifung von *Ascaris*. Arch. f. Zellforsch. **13**, 588—633, Taf. 38—40, 1 Fig. — Goodrich, H. B. (1914): The Maturation Divisions in *Ascaris incurva*. Biol. bull. of the marine biol. laborat. **27**, 147—150, 1 pl. — Ders. (1916): The Germ Cells in *Ascaris incurva*. Journ. of exp. zool. **21**, 61—99, 3 pl., 11 fig. — Guieysse-Pelissier, A. (1909): Etude de la division karyokinétique des cellules épithéliales de l'intestin d'*Ascaris megalocephala*. Cpt. rend. de l'assoc. anat. réun. **11**, 82—91, 4 fig. — Gulick, A. (1911): Über die Geschlechts-

chromosomen bei einigen Nematoden nebst Bemerkungen über die Bedeutung dieser Chromosomen. Arch. f. Zellforsch. **6,** 339—382, Taf. 18—20, 5 Fig. — Guyer, M. F. (1900): Spermatogenesis of Normal and Hybrid Pigeons. Ph. D. Thesis, U. of Chicago, 61 pp., 2 pl. — Ders. (1909a): The Spermatogenesis of the domestic Guinea (*Numida meleagris*). Anat. Anz. **34,** 502—513, Taf. 7—8. — Ders. (1909b): The Spermatogenesis of the domestic Chicken (*Gallus gallus*). Ebenda **34,** 573—580, Taf. 11—12. — Ders. (1910): Accessory Chromosomes in Man. Biol. bull. of the marine biol. laborat. **19,** 219—234, 1 pl. — Ders. (1916): Studies on the Chromosomes of the Common fowl as seen in testes and embryos. Ebenda **31,** 221—268, 7 pl. — Häcker, V. (1895): Über die Selbständigkeit der väterlichen und mütterlichen Kernbestandteile während der Embryonalentwicklung von *Cyclops*. Arch. f. mikroskop. Anat. **46,** 579—618, Taf. 28—30. — Ders. (1911): Allgemeine Vererbungslehre. Braunschweig 1911. 592 S., 4 Taf., 135 Fig. — Hance, R. T. (1917): The diploid chromosome complexes of the pig (*Sus scrofa*) and their variation. Journ. of morphol. **30,** 155—222, pl. 1—10, 5 fig. — Henking, H. (1891): Untersuchungen über die ersten Entwicklungsvorgänge in den Eiern der Insekten. II. Über Spermatogenese und deren Beziehung zur Eientwicklung bei *Pyrrhocoris apterus* L. Zeitschr. f. wiss. Zool. **51,** 685—736, Taf. 35—37, 1 Fig. — Hertwig, O. (1890): Vergleich der Ei- und Samenbildung bei Nematoden. Arch. f. mikroskop. Anat. **36,** 1—137, Taf. 1—4. — Hetherington, D. C. (1922): Some new methods in Nematode Technique. Journ. of karasitol. **9,** 102—104. — Jörgensen, M. (1910): Beiträge zur Kenntnis der Eibildung, Reifung, Befruchtung und Forschung bei Schwämmen (Syconen). Arch. f. Zellforsch. **4,** 163—242, Taf. 11—15, 1 Fig. — Jordan, H. E. (1911): The Spermatogenesis of the Opossum (*Didelphys virginiana*) with Special Reference to the Accessory Chromosome and the Chondriosomes. Ebenda **7,** 41—86, Taf. 1—3, 2 Fig. — Ders. (1916): The Spermatogenesis of the Mongoose, and a further Comparative Study of Mammalian Spermatogenesis, with Special Reference to Sex Chromosomes. Papers of the Tortugas laborat., Carnegie Instit., Wash. **5,** 163—180, 1 pl., 9 fig. — Kautzsch, G. (1912): Studien über Entwicklungsanomalien bei *Ascaris*. I. Arch. f. Zellforsch. **8,** 217 bis 251, Taf. 10—11, 43 Fig. — Ders. (1913): Studien über Entwicklungsanomalien bei *Ascaris*. II. Arch. f. Entwicklungsmech. d. Organismen **35,** 642 bis 691, Taf. 15—16, 63 Fig. — Kornhauser, S. I. (1914): A Comparative Study of the Chromosomes in the Spermatogenesis of *Enchenopa binotata* (Say) and *Enchenopa* (*Campylenchia* Stål) *curvata* (Fabr.). Arch. f. Zellforsch. **12,** 241—298, Taf. 18—22, 7 Fig. — Ders. (1915): A Cytological Study of the Semiparasitic Copepod, *Hersilia apodiformis* (Phil.), with some General Conclusions of Copepod Chromosomes. Ebenda **13,** 399—445, Taf. 27—29, 9 Fig. — Krimmel, O. (1910): Chromosomenverhältnisse in generativen und somatischen Mitosen bei *Diaptomus coeruleus*, nebst Bemerkungen über die Entwicklung der Geschlechtsorgane. Zool. Anz. **35,** 778—793, 16 Fig. — Kröning, F. (1923): Studien zur Chromatinreifung der Keimzellen. Die Tetradenbildung und die Reifeteilungen bei einigen Nematoden. Arch. f. Zellforsch. **17,** 63—85, Taf. 7—8. — Krüger, E. (1913): Fortpflanzung und Keimzellenbildung von *Rhabditis aberrans*, nov. sp. Zeitschr. f. wiss. Zool. **105,** 87—124, Taf. 3—6. — Kültz, K. (1913): Über die Spermio- und Oogenese der *Sclerostomum*-Arten des Pferdes unter besonderer Berücksichtigung der Heterochromosomenforschung. Arch. f. mikroskop. Anat. **83,** 191—266, Taf. 8—10, 8 Fig. — Kultschitzky, N. (1888): Über die Eireifung und die Befruchtungsvorgänge bei *Ascaris marginata*. Ebenda **32,** 671 bis 682, Taf. 26—27. — Lukjanow, S. M. (1889): Einige Bemerkungen über sexuelle Elemente beim Spulwurme des Hundes. Ebenda **34,** 397—408, Taf. 23—24. — Marcus, H. (1906): Ei- und Samenreife bei *Ascaris canis*. Ebenda

68, 441—490, Taf. 29—30, 10 Fig. — Matscheck, H. (1910): Über Eireifung und Eiablage bei Copepoden. Arch. f. Zellforsch. **5,** 36—119, Taf. 4—8, 30 Fig. — Mayer, A. (1908): Zur Kenntnis der Samenbildung bei *Ascaris megalocephala*. Zool. Jahrb., Abt. f. Anat. **25,** 495—546, 2 Taf., 2 Fig. — Mc Clung, C. E. (1902): The Accessory Chromosome — sex determinant? Biol. Bull. of the marine biol. laborat. **3,** 43—84. — Mc Dowell, S. A. (1906): A Preliminary Note on the Miotic Phenomena in the Eggs of the Hermaphrodite „*Angiostomum nigrovenosum*" („*Ascaris nigrovenosa*"). Proc. of the Cambridge philos. soc. **13,** 309—312, pl. 4. — Meves, F. (1915): Über Mitwirkung der Plastosomen bei der Befruchtung des Eies von *Filaria papillosa*. Arch. f. mikroskop. Anat. **87,** 12—46, Taf. 1—4. — Ders. (1921): Über Samenbildung und Befruchtung bei *Oxyuris ambigua*. Ebenda **94,** 135—184, Taf. 9—13. — Meyer, O. (1895): Celluläre Untersuchungen an Nematodeneiern. Jenaische Zeitschr. f. Naturwiss., 29. N. F., **22,** 391—410, Taf. 9—10. — Montgomery, T. H. jr. (1901): A Study of the Germ Cells of Metazoa. Transact. of the Americ. philos. soc. **20,** 54—236, pl. 4—8. — Ders. (1908): On Morphological Difference of the Chromosomes of *Ascaris megalocephala*. Arch. f. Zellforsch. **2,** 66—75, Taf. 6—7. — Mulsow, K. (1912): Der Chromosomencyclus bei *Ancyracanthus cystidicola*. Ebenda **9,** 63—73, Taf. 5—6, 5 Fig. — Nachtsheim, H. (1913): Cytologische Studien über die Geschlechtsbestimmung bei der Honigbiene (*Apis mellifica*). Ebenda **11,** 169—241, Taf. 7—10. — Paulmier, F. C. (1899): The Spermatogenesis of *Anasa tristis*. Journ. of morphol. **15,** (Suppl.), 223—272, pl. 13 to **14.** Schleip, W. (1911): Das Verhalten des Chromatins bei *Angiostomum* (*Rhabdonema*) *nigrovenosum*. Ein Beitrag zur Kenntnis der Beziehungen zwischen Chromatin und Geschlechtsbestimmung. Arch. f. Zellforsch. **7,** 87 bis 138, Taf. 4—8. — Ders. (1912): Geschlechtsbestimmende Ursachen im Tierreich. Ergebn. u. Fortschr. d. Zool. **3,** 165—328, 22 Fig. — Seiler, J. (1913): Das Verhalten der Geschlechtschromosomen bei Lepidopteren. Zool. Anz. **41,** 246—251, 4 Fig. — Sinéty, R. de (1901): Recherches sur la biologie et l'anatomie des Phasmes. La cellule. **19,** 119—278, 5 pl. — Smith, G. (1912): Studies in the Experimental Analysis of Sex. Part 9. On Spermatogenesis and the Formation of Giant Spermatozoa in Hybrid Pigeons. Quart. journ. of microscop. science, N. S. **58,** 159—171, pl. 8. — Strassen, O. zur (1896): Embryonalentwicklung der *Ascaris megalocephala*. Arch. f. Entwicklungsmech. d. Organismen **3,** (1), 27—105, **3,** (2), 133—190, Taf. 5—9, 29 Fig. — Struckmann, C. (1905): Eibildung, Samenbildung und Befruchtung von *Strongylus filaria*. Zool. Jahrb., Abt. f. Anat. **22,** 577—628 Taf. 29—31, 18 Fig. — Taylor, M. (1917): The Chromosome Complex of *Culex pipiens*. Quart. journ. of microscop. science **62,** 287—301, pl. 20, 1 fig. — Walton, A. C. (1916a): *Ascaris canis* (Werner) and *Ascaris felis* (Goeze). A Taxonomic and a Cytological Comparison. Biol. bull. of the marine biol. laborat. **31,** 364—371, pl. 1, 6 fig. — Ders. (1916b): A Case of the Occurrence of *Ascaris triquetra* Schrank in Dogs. Journ. of parasitol. **3,** 39—41, 6 fig. — Ders. (1918): The oögenesis and early embryology of *Ascaris canis* Werner. Journ. of morphol. **30,** 527—603, 9 pl., 1 fig. — Ders. (1921): The Spermatogenesis of *Ascaris felis* (Goeze). Journ. of exp. zool. **34,** 189—201, 2 pl. — Ders. (1923): A description of four new species and a report on new American Place Records for some little known Nematodes. Journ. of parasitol. **10,** 59—70, 2 pl. — Wilson, E. B. (1906): Studies on Chromosomes III. The Sexual Difference of the Chromosome Groups in *Hemiptera*, with special Considerations on the Determination and Inheritance of Sex. Journ. of exp. zool. **3,** 1—40, 6 fig. — Ders. (1909): Studies on Chromosomes IV. The „Accessory" chromosome in *Syromastes* and *Pyrrochoris* with a Comparative Review of the Types of Sexual Differences of the Chromosome Groups. Ebenda **6,** 69—100,

2 pl., 2 fig. — Wodsedalek, J. E. (1913): Spermatogenesis of the Pig, with special reference to the Accessory Chromosomes. Biol. bull. of the marine biol. laborat. **25,** 8—46, pl. 1—6, 1 fig. — Ders. (1914): Spermatogenesis of the Horse with Special Reference to the Accessory Chromosome and the Chromatoid Body. Biol. Bull., **27,** 295—324, 6 pls., 1 fig. — Ders. (1920): Studies on the Cells of Cattle with Special Reference to Spermatogenesis, Oögonia, and Sex-Determination. Biol. Bull., **38,** 290—316, 5 pls., 1 fig. — Zacharias, O. (1912): Eine neue Varietät des Pferdespulwurms (*Ascaris megalocephala*, var. *trivalens*). Biol. Zentralbl. **32,** 718—721, 1 Fig. — Ders. (1913a): Die Chromatindiminution in den Furchungszellen von *Ascaris megalocephala*. Anat. Anz. **43,** 33—53, 15 Fig. — Ders. (1913b): Über Variationen der Chromosomenzahl im Mutterstern des Eies von *Ascaris megalocephala*. Zool. Anz. **41,** 174—175.

VIII. Explanation of plates.

All the figures in Plates 1 to 4 were drawn with the aid of a camera lucida, the projection distance being 450 mm. Leitz $^1/_{12}$ oil immersion objective and compensating ocular 3× and 12× were used.

Abbreviations.

The following abbreviations are employed: —

H., heterochromosome
p., propagation cell
s., First soma cell.

Plate VIII.

All figures were magnified 3000 diametra, and are reduced by one-fourth.

Contracaecum spiculigerum.

1. Prophase nucleus, first spermatocyte, showing formation of eight chromosomes.
2. Metaphase plate, first spermatocyte, showing eight chromosomes.
3. Metaphase plate, second spermatocyte, showing seven tetrad chromosomes.
4. Metaphase plate, second spermatocyte, showing eight tetrad chromosomes.
5. Spermatid, showing eight dyad chromosomes and peripheral layer of heavily staining nutritive material.
6. Spermatid surrounded by extruded glycogen material.
7. Spermatozoa with adjacent 'cytophore' material.
8. Mature spermatozoon.
9. Prophase nucleus, first oocyte, showing eight dyad diploid chromosomes.
10. Metaphase plate, first oocyte, showing eight di-tetrad chromosomes.
11. Metaphase plate, second oocyte, showing eight tetrad chromosomes.
12. Telophase plate, second oocyte, showing eight dyad chromosomes.

Ascaris lumbricoides.

13. Metaphase plate of soma cell from female producing embryo, showing forty-eight monad chromosomes after the 'diminution' division.
14. Metaphase plate of soma cell from male producing embryo, showing forty-three monad chromosomes after the 'diminution' division.

Belascaris mystax.

15. Prophase nucleus, first oocyte, showing formation of discrete chromosomes.
16. Metaphase plate, second oocyte, showing idiochromosome attached to the end of one of the nine dyad autosomes.
17. Male and female pronuclei, each showing nine autosomes and the attached idiochromosome.
18. Male and female pronuclei, the male pronucleus lacking the idiochromosome.
19. Fusion nucleus showing presence of eighteen monad autosomes and two attached idiochromosomes.
20. Fusion nucleus showing presence of eighteen monad autosomes and only one attached idiochromosome.
21. Metaphase plates of soma cells after having undergone diminution.
    a) Eighteen small autosomes and one attached idiochromosome.
    b) Eighteen small autosomes and two attached idiochromosomes.

Belascaris triquetra.

22. Prophase nucleus, first spermatocyte, showing resolution of discrete chromosomes from chromatin mass. Heterochromosome at the lower left.
23. Anaphase plate, first spermatocyte, containing ten tetrad autosomes and two tetrad idiochromosomes.
24. Anaphase plate, first spermatocyte, containing ten tetrad autosomes.
25 *a* and *b*. Daughter plates of second spermatocytic division showing ten dyad autosomes and two dyad idiochromosomes.
26 *a* und *b*. Daughter plates of second spermatocytic division showing ten dyad autosomes.
27. Prophase nucleus, first oocyte, showing formation of discrete chromosomes from chromatin mass. Heterochromosome group (?) to upper left.
28. Prophase nucleus, first oocyte, showing formation of twenty-four tetrad chromosomes, each with a Querkerbe and a single longitudinal split.
30. Metaphase plate, first oocyte, showing twelve di-tetrad chromosomes.

Plate IX.

All Figures were magnifrid 3000 diameters and are reduced by one-forrth.

Belascaris triquetra.

29. First maturation spindle in the center of the egg (× 1010).
31. Telophase plate, first oocyte, showing twelve tetrad chromosomes.
32. Four-celled embryo showing simultaneous diminution divisions in the daughter calls of the first 'soma' cell. Second 'soma' cell at *s.*, and the 'propagation' cell at *p.*
33. Metaphase plate in a soma cell which has undergone 'diminution', showing double the diploid number of monad chromosomes.

Toxascaris canis.

34. Spermatogonial cell showing two unequal karyosomes.
35. Prophase, first spermatocyte, showing resolution of discrete chromosomes from the chromatin mass. Heterochromosome group to the right.
36. Polar view of metaphase plate, first spermatocyte, showing twelve di-tetrad autosomes and six tetrad heterochromosomes.
37. Prophase nucleus, first oocyte, showing resolution of discrete chromosomes from chromatin mass.
38. Prophase nucleus, first oocyte, showing longitudinal split in the thirty-six dyad chromosomes.

39. Metaphase plate, first oocyte, showing eighteen tetrad chromosomes.
40. Metaphase plate, male producing zygote, showing thirty dyad chromosomes.
41. Metaphase plate, female producing zygote, showing thirty-six dyad chromosomes.
42. Metaphase plate, soma cell after undergoing 'diminution', showing double the number of diploid chromosomes of the male — sixty monads.
43. Metaphase plate, soma cell after undergoing 'diminution', showing double the number of diploid chromosomes of the female — seventy-two monads.

Ganguleterakis spumosa.

44. Prophase nucleus, first spermatocyte, showing four di-tetrad autosomes and two smaller tetrad heterochromosomes.
45. Metaphase plate, first spermatocyte.
46. Late anaphase spindle, first spermatocyte, showing lagging heterochromosome.
47. Sister cells, second spermatocytes, showing one with four tetrad autosomes and the other with four tetrad autosomes and two tetrad heterochromosomes.
48. a) Spermatid having four dyad chromosomes.
    b) Spermatid having six dyad chromosomes.
49. Prophase, first oocyte, showing twelve tetrad chromosomes, each with a Querkerbe and a single longitudinal cleft.
50. Late prophase, first oocyte, showing six di-tetrad chromosomes, formed by parasyndesis of twelve tetrads.
51. Metaphase plate, second oocyte, showing six tetrad chromosomes.
52. Telophase plate, second oocyte, showing six dyad chromosomes.
53. Fusion nucleus showing ten dyad chromosomes.
54. Fusion nucleus showing twelve dyad chromosomes.
55. Some cell after first division, showing double the diploid number of monad chromosomes.

Heterakis papillosa.

56. Spermatogonium showing eighteen monad chromosomes.
57. Prophase, first spermatocyte, showing five haploid chromosomes.
58. Metaphase plate, first spermatocyte, showing four di-tetrad and one tetrad chromosomes.
59 *a* and *b*. Metaphase plates, second spermatocytes, showing four and five tetrad chromosomes.
60 *a* and *b*. Telophase plates, second spermatocytes, showing four and five dyad chromosomes.

Plate X.

All figures were magnified 3000 diameters, and are reduced by one-fourth.

Heterakis papillosa.

61. Spermatozoon.
62. Metaphase plate, first oocyte, showing five di-tetrad chromosomes.
63. Anaphase spindle, second oocyte, showing five dyad chromosomes in each plate.
64. Nucleus of intestinal cell from adult male, showing eighteen monads; double the diploid number of chromosomes.

Physaloptera turgida.

65. Metaphase plate, first spermatocyte, showing five tetrad chromosomes.
66. Telophase spindle, first spermatocyte, showing lagging of heterochromosome and accompanying autosome.
67 *a* and *b*. Metaphase plates of the two types of second spermatocytes, showing four and five dyad-like chromosomes respectively.
68 *a* and *b*. Telophase plates of the two types of second spermatocytes, showing four and five dyad chromosomes respectively.
69. Prophase nucleus, first oocyte, showing five chromatin bodies and two plasmosomes.
70. Metaphase plate, first oocyte, showing five dyad chromosomes.
71. Anaphase spindle, first oocyte, showing peculiar lagging of two chromosomes.
72. Metaphase plate, second oocyte, showing five dyad chromosomes.
73. Telophase plate, second oocyte, showing five dyad chromosomes.
74. Pronuclei; male with four and female with five dyad chromosomes.
75. Pronuclei; each with five dyad chromosomes.
76. Metaphase plate, fusion nucleus of male-producing zygote, showing nine dyad chromosomes.
77. Metaphase plate, fusion nucleus of female-producing zygote, showing ten dyad chromosomes.
78. Embryo having ten dyad chromosomes — female producing.

Plate XI.

All figures were magnified 3000 diameters, and are reduced by one-fourth.

Physaloptera turgida.

79. Embryo having nine dyad chromosomes — male producing.
80. Embryo showing dyad chromosomes in 'propagation' cell '*p*', and double the number of monad chromosomes in a somatic cell.

Protospirura muris.

81. Metaphase plate, first spermatocyte.
82. Metaphase plate, second spermatocyte, showing four tetrad autosomes.
83. Metaphase plate, second spermatocyte, showing four tetrad autosomes and one tetrad idiochromosome.
84 and 85. Anaphase plates of secondary spermatocyte, showing four and five dyad chromosomes, respectively.
86. Metaphase plate, first oocyte, showing five di-tetrad chromosomes.
87. Metaphase plate, second oocyte, showing five tetrad chromosomes.
88. Anaphase plate, second oocyte, showing five dyad chromosomes.
89. Metaphase plate, fusion nucleus, with nine dyad chromosomes.
90. Metaphase plate, fusion nucleus, with ten dyad chromosomes.

Cruzia tentaculata.

91. Interkinetic stage, growth period of primary oocyte, showing distinct heterochromosome failing to break up as do the autosomes.
92. Late prophase, first spermatocyte, showing double nature of the heterochromosome and the formation of ten autosomes.
93. Metaphase plate, first spermatocyte.
94. Anaphase spindle, first spermatocyte, showing lagging heterochromosome.
95. Metaphase plate, second spermatocyte, showing five tetrad chromosomes.

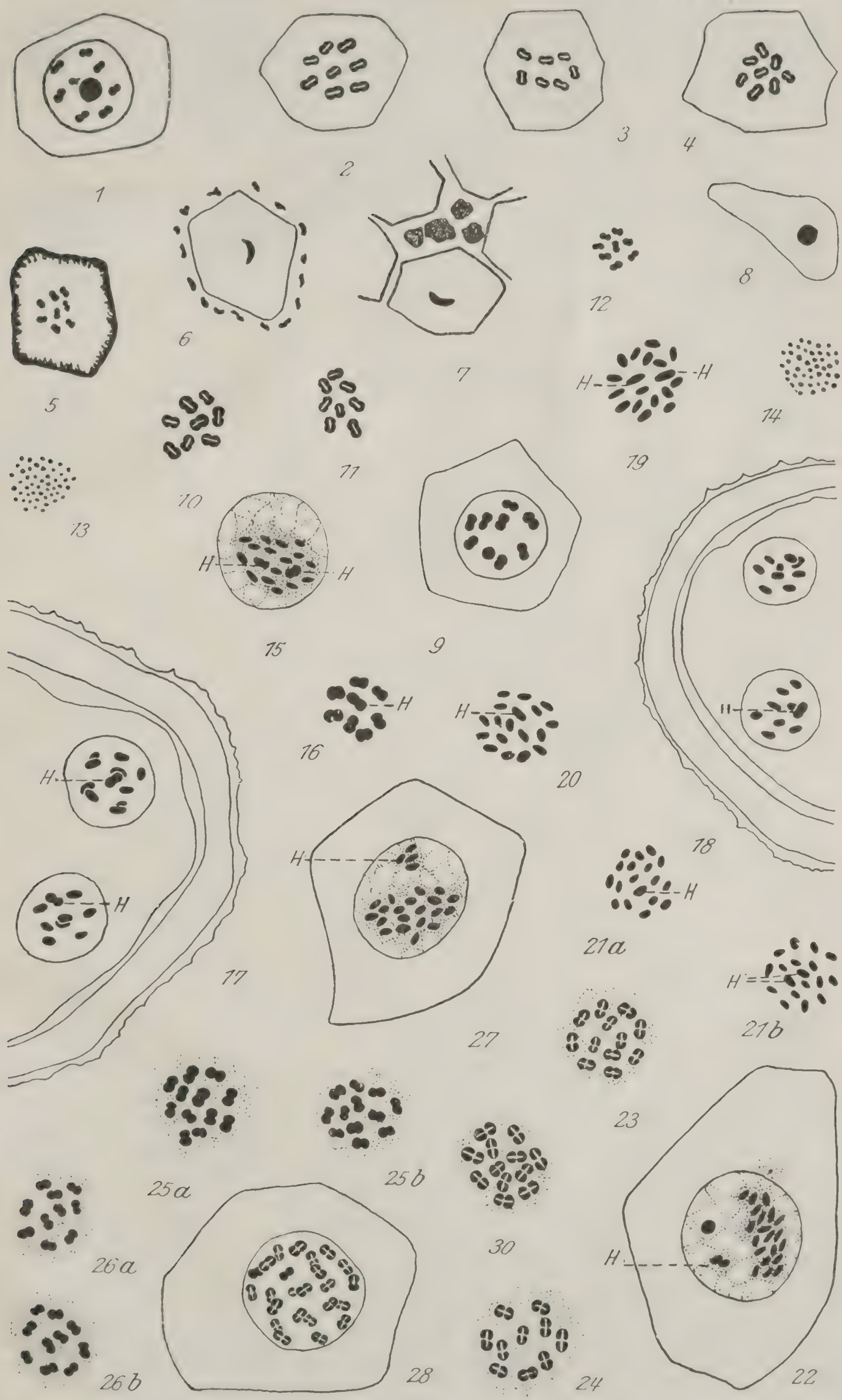
96. Metaphase plate, second spermatocyte, showing six tetrad chromosomes.
97. Spermatid showing five dyad chromosomes.
98. Spermatid showing six chromosomes.
99. Metaphase plate, first oocyte, showing six di-tetrad chromosomes.
100. Metaphase plate, second oocyte, showing six tetrad chromosomes.
101. Male pronucleus showing six dyad chromosomes.
102. Female pronucleus showing six dyad chromosomes.
103. Male pronucleus showing five dyad chromosomes.

Nematospira turgida.

104. Prophase nucleus, first spermatocyte, showing independant position of the heterochromosome during syndesis.
105. Metaphase plate, first spermatocyte, showing heterochromosome at the edge of the group.
106. Metaphase plate, second spermatocyte, showing five tetrad chromosomes.
107. Metaphase plate, second spermatocyte, showing six tetrad chromosomes.
108. Spermatozoa, showing hollow nature of the 'Glanzkörperchen'.
109. Metaphase plate, first oocyte, showing six di-tetrad chromosomes.
110. Metaphase plate, second oocyte, showing six tetrad chromosomes.

Trichosomoides crassicauda.

111. Prophase nucleus, first spermatocyte, showing four tetrad chromosomes.
112. Metaphase plate, first spermatocyte, showing four tetrad chromosomes.
113. Metaphase plate, second spermatocyte, showing three tetrad chromosomes.
114. Metaphase plate, second spermatocyte, showing four tetrad chromosomes.
115. Spermatozoon, showing whip-like tail and absence of 'Glanzkörperchen'.
116. Oogonial cell showing eight 'V'-shaped chromosomes.
117. Metaphase plate, first oocyte, showing four di-tetrad chromosomes.
118. Metaphase plate, second oocyte, showing four tetrad chromosomes.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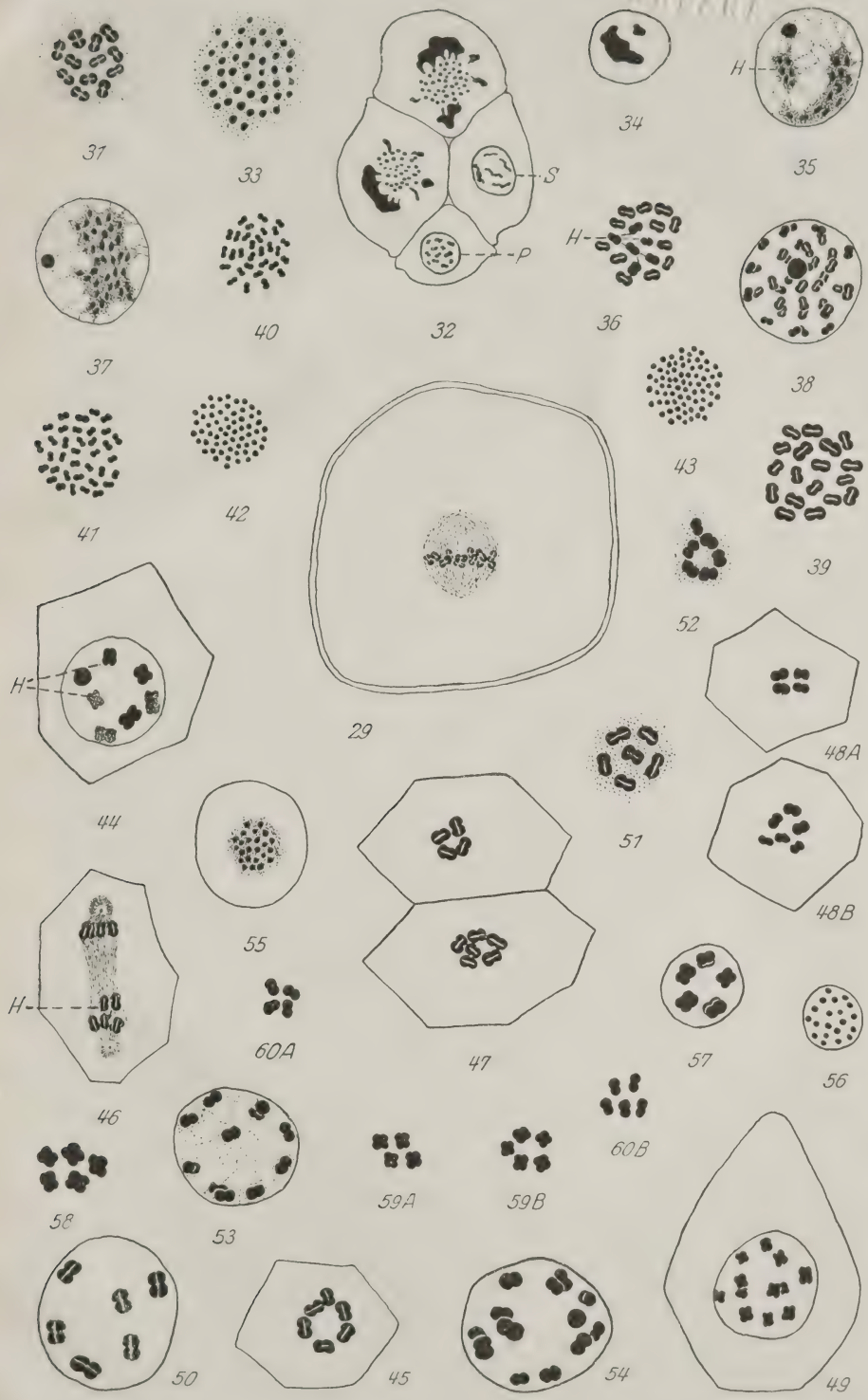
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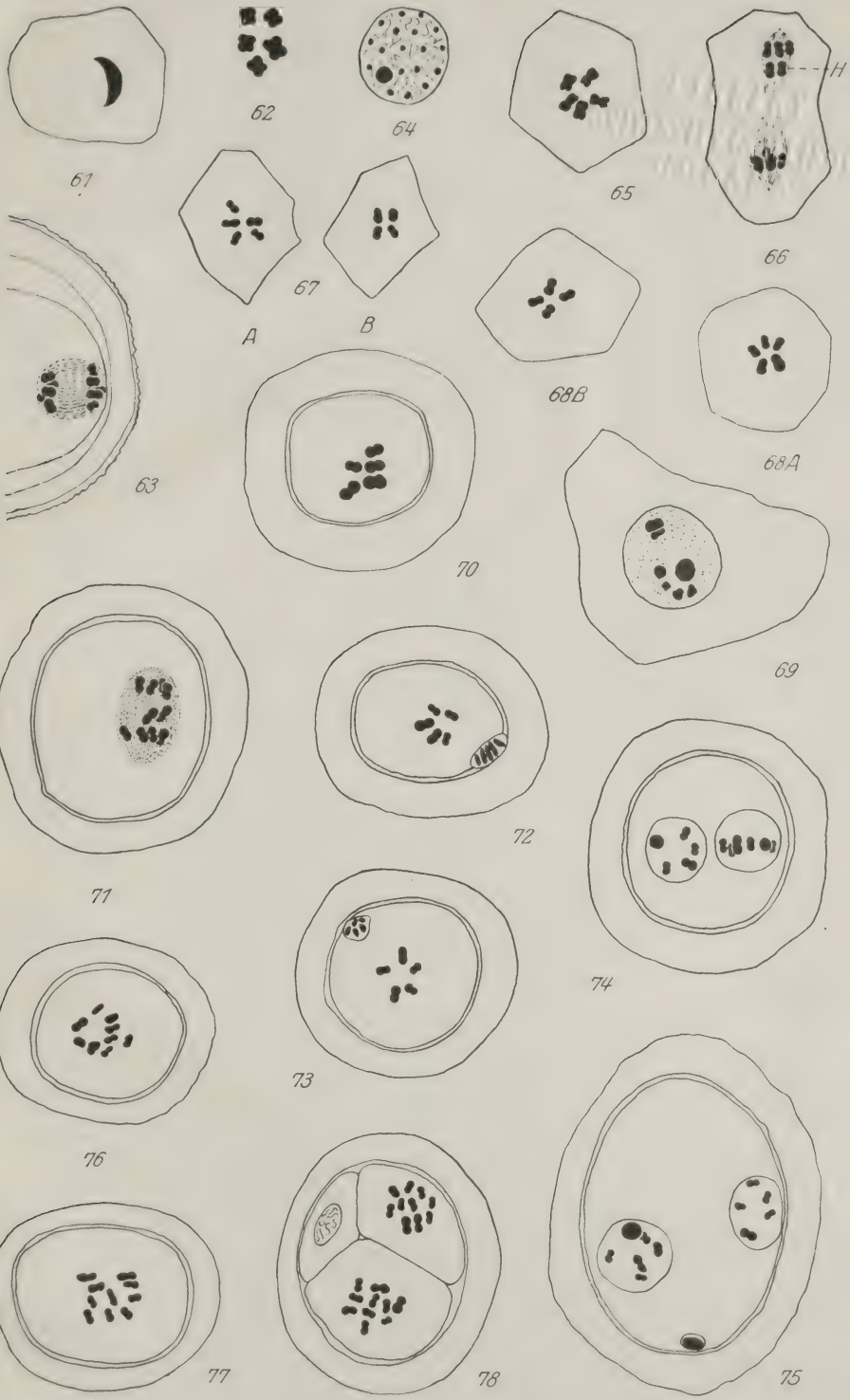
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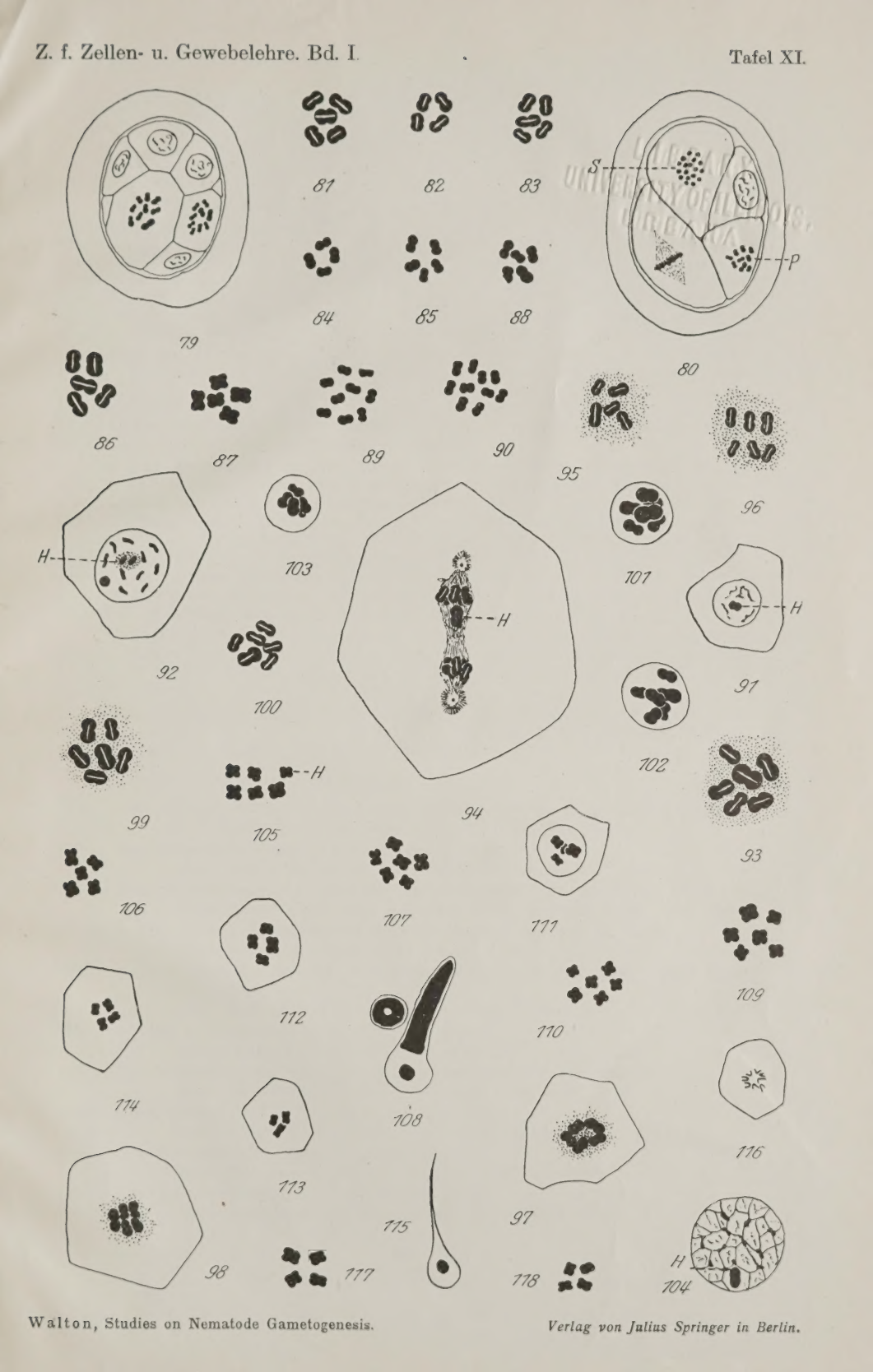
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VITA

Arthur C. Walton was born October 16, 1892, at Meadville, Penna. He attended the public schools of Chicago, Illinois, graduating from Lake View High School in June, 1909. His undergraduate College work was taken at Northwestern University, Evanston, Illinois, graduating with a degree of B.A. *cum laude* in June, 1914. He was awarded the Master of Arts degree in Zoology from the same institution in June, 1915. Two years of graduate study in Zoology at Harvard University followed. He was appointed Associate Professor of Biology at North Western College, Naperville, Illinois, for the second semester of 1917-18, leaving there in June for the army. After serving a year in France in the Medical Service, he returned to North Western College in September, 1919, as Professor of Biology. In 1920 he was appointed Professor of Zoology and the Head of the Department of Biology. A leave of absence to complete the requirements for a Ph.D. degree was granted for the academic year of 1922-23, and has been spent at the University of Illinois, Urbana, Illinois.

He was student assistant in Zoology at Northwestern University during 1912-13 and 1913-14; he received a University Scholarship and acted as Graduate Assistant at Northwestern during 1914-15. He was appointed "Virginia Barrett Gibbs Scholar in Marine Biology" at Harvard University in 1915-16, and "Austin Teaching Fellow" in Zoology at Harvard for 1916-17. He acted as part time instructor at Radcliffe College, Cambridge, Mass., 1915-17. Appointment as an "Austin Traveling Fellow" from Harvard for 1917-18 was awarded but not made use of because of war conditions. He has acted as Graduate Assistant in Zoology at the University of Illinois during 1922-23.

The summers of 1913 and 1914 were spent at the Marine Biological Station, Woods Hole, Mass., on scholarships from Northwestern University, and the summer of 1916 at the Bermuda Biological Station at Agara Island, B. W. I., on a scholarship from Harvard University.

He is a member of the North Central Association of Science and Mathematics Teachers; Sigma Xi; American Association for the Advancement of Science, Section F; and the American Society of Zoologists.

His publications are as follows:

1915. The Influence of Diverting Stimuli during Delayed Reactions in Dogs.
Jour. Anim. Behavior, 6(4):259-291. July-Aug. 1915.

1916. Reactions of Paramoecium caudatum to Light.
Jour. Anim. Behavior, 6(5):335-340. Sept.-Oct. 1916.

1916a. The "Refractive Body" and the "Mitochondria" of Ascaris canis Werner.
Proc. Amer. Acad. Arts and Sci., 52(5):253-266, 2 pls. Oct. 1916.

1916b. A Case of the Occurrence of Ascaris triquetra Schrank in Dogs.
Jour. Parasitol. 3(1):39-41. Sept. (Oct.) 1916.

1916c. Ascaris canis Werner and Ascaris felis Goeze. A Taxonomic and a Cytological Comparison.
Biol. Bull., 31(5):364-372, 1 pl. Nov. 1916.

1917. A Case of Regeneration in Panulirus argus.
Amer. Nat., 51(605):308-310. May 1917.

1918. The Oogenesis and Early Embryology of Ascaris canis Werner.
Jour. Morph., 30(2):527-603, 9 pls. Mar. 1918.

1918a. Longitudinal Fission in Actinia bermudensis Verrill.
Jour. Morph., 31(1):43-52, 1 pl. June 1918.

1921. The Nematodes as Teaching Material.
School Sci. and Math., 21(10):565-572. June 1921.

1921a. The Spermatogenesis of Ascaris felis Goeze.
Jour. Exp. Zool., 34 (2):189-201, 2 pls. Oct. 1921.